

1968

Allegheny (Pennsylvanian) Conodonts.

Glen Kenton Merrill

Louisiana State University and Agricultural & Mechanical College

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ALLEGHENY (PENNSYLVANIAN) CONODONTS

A Dissertation

Submitted to the Graduate Faculty of the
Louisiana State University and
Agricultural and Mechanical College
in partial fulfillment of the
requirements for the degree of
Doctor of Philosophy

in
The Department of Geology

by
Glen K. Merrill
B.S., Ohio University, 1957
M.A., The University of Texas, 1964
August 1968

MANUSCRIPT THESES

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F R O N T I S P I E C E

WASHINGTONVILLE LOCALITY 10

Panoramic view of Washingtonville locality 10 (arbitrary locality number 52, Ferm's locality Coshocton 20, $40^{\circ}15'45''\text{N}$, $81^{\circ}53'24''\text{W}$) illustrating several characteristics of abandoned strip mines in eastern Ohio. The objective of the mining, the Middle Kittanning (#6) Coal is presently below water level, but conodont-bearing Washingtonville Shale could, at the time the photograph was taken, be dug out of the badly slumped high wall just above water level.

photograph: G.K. Merrill, August 1965

A C K N O W L E D G M E N T S

To the members of my committee: Dr. John C. Ferm, supervisor, Dr. H.V. Andersen, Dr. George F. Hart, Dr. James P. Morgan, Dr. Bobby F. Perkins, and Dr. Carl B. Rexroad of the Indiana Geological Survey (outside specialist), I wish to express gratitude for their efforts to improve the final quality of this dissertation. Doctor John C. Ferm deserves special thanks for supervision, counsel, and guidance at all stages of the work. The *geology* in this dissertation bears the unmistakable stamp of his influence; he can in no way be blamed for the *paleontology*. George Hart performed a remarkably detailed and highly appreciated editing job, far beyond that normally expected from a committee member. Access to, and assistance with, the camera equipment used to photograph the conodonts were provided by Dr. Perkins. As the conodont specialist on the committee, Carl Rexroad played a most important rôle by assuring that the systematics portion, if not brilliant, at least was within the realm of acceptability to "conodontists" in general. Moreover, he too did a very detailed editing job for which, because he is not associated with Louisiana State University, his only recompense is my sincere thanks.

Several of Dr. Ferm's students, past and present, assisted by providing not only locality information, but a number of samples as well. "Fermites", the local appellation for them, who contributed in those ways include: Dr. Romeo M. Flores, Mr. David E. Pedersen, Mr. Harry H. Roberts, and Dr. Ronald K. Zimmerman.

Doctor Prentiss Schilling, Department of Experimental Statistics, assisted with discussions of test design and several persons

in the L.S.U. Computer Center, notably Dr, E.L. Morton, Mr. Sidney O. Smith, Mr. Robert Dixon, and Mr. James Steele, either wrote programs, modified existing ones, or generally helped in getting my work completed.

A special sort of thanks is due Prof. and Mrs. George B. Corrie of Huntington, West Virginia who permitted me to use their home as a base of operations during the 1965 field season.

Property owners, strip mine operators, and others graciously cooperated in the field. Most of these are namesless individuals, but I would like to cite a pair of examples. Personnel of the Porter Pottery at Merrill, Pennsylvania not only permitted me to collect from a section there, but willingly provided all the fiber drums necessary to ship the several hundred pounds of samples to Louisiana. Meanwhile, these samples were being stored for me by the people at the Humble Oil Company Bulk Station in East Liverpool, Ohio awaiting shipment.

The usual tribute paid by a thesis writer to his wife for her forbearance and typing assistance is trite and totally inadequate for Stina's many contributions to this work. She assisted in the field, in the laboratory by washing nearly every shale sample used, that alone being hundreds of hours work, did all the drafting, and assisted in typing, proofreading, and editing the many manuscript drafts. Most important, however, were her loving kindness, co-operation, and understanding during a long and arduous preparation.

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A B S T R A C T

Variations in Allegheny conodonts are the results of temporal, regional, and local influences. Biostratigraphic zonation presently must be based mostly on the phylogeny of the genus *Gnathodus* rather than the more abundant *Idiognathodus-Streptognathodus* lineage. Complete transitions from *Gnathodus bassleri* in the underlying Pottsville through three new species to *Gnathodus roundyi* and *G. dilatus* in the upper Allegheny permit the recognition of three zones in the Allegheny and two in the upper Pottsville. The highest of the Allegheny zones contains too few gnathodids to employ them for zonation and is recognized instead by the large influx of streptognathodids, forming a link with the succeeding Conemaugh faunas.

Provincialism between "Appalachian" and "Midcontinent" taxa is exhibited for the Allegheny in the same manner as for the Conemaugh faunas. The two groups of taxa are regionally distributed in patterns illustrating intermingling of segregated, contemporaneous populations. The common Midcontinent genus *Gondolella* has not been found in the Appalachians among more than 100,000 (46,508 from this study) specimens and presumably represents the most restricted taxon among Midcontinent forms.

Allegheny conodont biofacies, involving *Cavusgnathus* and *Idiognathodus*, exactly parallel those from the Conemaugh between *Cavusgnathus* and *Streptognathodus*. Differences in the ratios

of the two genera are commonly found regionally within a stratigraphic unit, between closely spaced outcrops within the unit, or within the unit in a single outcrop. These final, within outcrop, examples may be either vertically succeeding biofacies or lateral equivalents and are perhaps the most compelling evidence for conodont biofacies yet presented. Vertical changes may increase or decrease the relative abundance of the two genera tenfold across a bedding plane. Lateral examples may accomplish the same thing over distances of a few hundred feet.

INTRODUCTION

PURPOSE AND SCOPE

This dissertation is an extension of my previous work (Merrill, 1962, 1964, 1966) with the Upper Pennsylvanian Conemaugh conodonts. It includes the Middle Pennsylvanian Allegheny Group conodont faunas. As such, it includes another major segment of the Pennsylvanian rocks of the Appalachian region, those which underly the Conemaugh Group. The scope of this dissertation includes descriptions of all observed Allegheny conodont occurrences, interpretations of their meanings, and their systematic treatment.

Previous knowledge, based on published works of others, as well as my experience with the Conemaugh conodonts, permitted framing several hypotheses about the distribution of conodonts in the Allegheny. If the distributions of Allegheny conodonts are similar to those of the Conemaugh, certain faunal differences may be predicted between stratigraphic units based on phylogenetic changes. In addition, other differences may be expected within stratigraphic units on the scale of a single outcrop or between closely spaced outcrops as a result of environmental or biofacies differences, and still others on a regional scale within or between basins which most likely are the product of provincial differences. Finally, it can be reasonably expected that some taxa will be unaffected by any of the above factors and thus truly ubiquitous.

To test these hypotheses, samples were taken from the best known marine stratigraphic units over their entire outcrop areas. At least 24 localities were sampled for each of the four productive units.

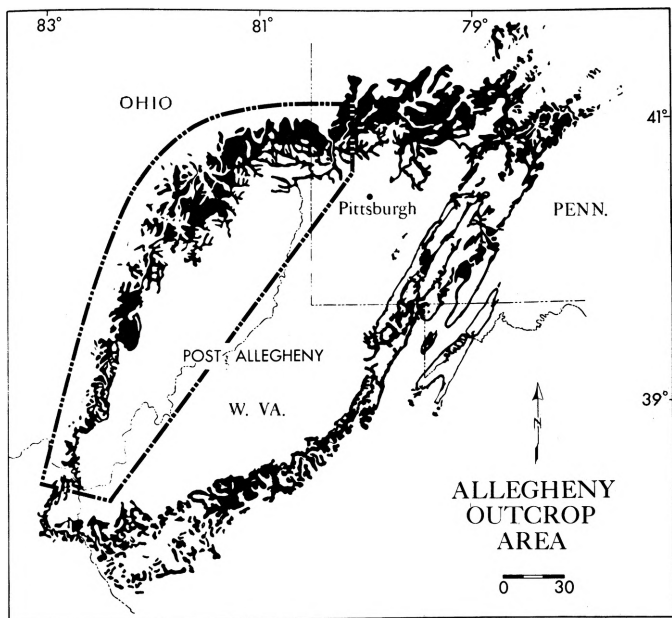
In order to assess within outcrop faunal variations, every individual bed containing marine macrofossils at each locality was sampled. The conodonts obtained from these samples were assigned to a large number of taxonomic categories, and the individuals in each category were counted and recorded. Reduction in the number of these categories, through combinations based on observed mutual occurrences, produced 21 broader categories, most of them at the generic level.

Both simple observation and statistical testing confirmed the tendency for these categories to form four distinct groups, the taxa of which most commonly occur together. Three of these four groups conform to the expected patterns of biofacies and provincial faunas, and the fourth, ubiquitous one, contains the desired phylogenetic changes useful for biostratigraphy.

RESUME OF PENNSYLVANIAN CONODONT RESEARCH

Unlike paleontologic studies of several other Paleozoic systems, conodont research in Pennsylvanian rocks has been almost entirely descriptive with only minor biostratigraphic and phylogenetic work. The earliest descriptive paper on Pennsylvanian conodonts was by Gunnell (1931) who named several species from a sample of the Anna Member (Pawnee Formation, Desmoinesian Series) of Missouri. Stauffer and Plummer added several more taxa from Desmoinesian rocks of central and north-central Texas in 1932. Harris and Hollingsworth (1933) and Harlton (1933) added some genera and species from presumed pre-Desmoinesian rocks of Oklahoma. Gunnell's second paper (1933) included material from a few samples of Desmoinesian through Lower Permian rocks and greatly proliferated the number of Pennsylvanian conodont

Figure 1. Map of Allegheny outcrop area. Area of collecting shown.
(after Ferm, files)



species.

The most noteworthy paper in this period was by Ellison (1941) who drastically reduced the large number of taxa by placing similar morphologic forms into synonymy, thereby creating a framework for his own morphologic classification. This paper also marked the earliest attempt to define the stratigraphic ranges of genera and species and therefore has broad-scale biostratigraphic application. Nonetheless, Ellison did not specifically zone the Desmoinesian through Virgilian column that he described.

Cooper (1947) attempted to interpret from Ellison's work a series of zones based on characteristic species, but his work has not been generally accepted and cannot be applied advantageously to the Appalachian material.

Since Ellison's revisionary work, relatively few papers dealing with Pennsylvanian conodonts have appeared. With few exceptions these have been descriptive, have dealt with few specimens from restricted intervals or single samples, and have provided little phylogenetic data. The result has been another substantial increase in the number of species, most of which are based on differences which Ellison apparently considered too unimportant to distinguish. Two recent papers dealing with Upper Mississippian and Lower Pennsylvanian conodont faunas by Koike and by Lane (both July 1967) probably will have a profound affect upon future work with Lower Pennsylvanian conodonts.

There are few references to Pennsylvanian conodonts from the Appalachians. Sturgeon and Youngquist (1949) published on some Allegheny conodonts from the Columbiana and Washingtonville Members

of eastern Ohio. Merrill (1964) proposed a zonation for the Conemaugh Group, the approximate Missourian and Virgilian equivalent in the Appalachians. That study treated only certain taxa, their phylogenies, and some paleoecologic implications of faunal differences. This experience showed that Ellison's morphospecies can be used to divide the seven Conemaugh marine zones into four biostratigraphic zones.

Ellison's work (1941) remains the most comprehensive done on Pennsylvanian conodonts and is the one with which all future works will be compared. The most important attributes and contributions of his work were:

- 1) Ellison's collections were large, although no counts were given for the individual taxa or the total number of specimens. His collections have not been equalled in size until the present, probably larger, ones from the Conemaugh and Allegheny.

- 2) His material covered a large stratigraphic interval.

- 3) He reduced a cluttered taxonomy to a minimum number of taxa with potential usefulness.

- 4) In accomplishing 3), he redescribed the taxa he retained to the extent that our concepts of them are more dependent on his work than on the descriptions of the original authors.

- 5) This is the only work on Pennsylvanian conodonts to summarize the ranges of genera and species.

Despite these major contributions, his work had several limitations:

- 1) All of Ellison's material came from the Midcontinent region and much of it was further restricted geographically to

a few small areas such as those around Columbia, Missouri, and Kansas City, Missouri-Kansas.

2) Although his samples were spread through a large stratigraphic interval, all of them were shales. Large-scale acetic acid digestion of limestones had not been begun at that time. This was partially responsible for the fact that most of Ellison's samples came from very few intervals and the majority of the column was not adequately sampled.

3) No actual zonation was proposed in this work, despite several generalizations about the ranges and abundances of individual taxa.

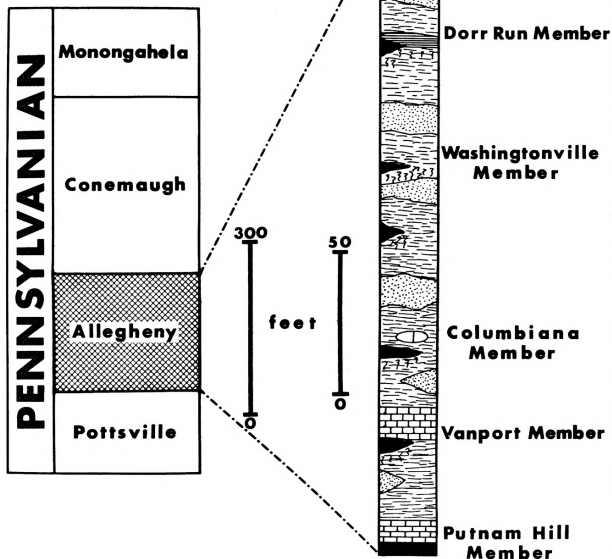
4) Although many taxa were described or redescribed by Ellison, there are many others not described in his study. This omission can be partially explained by the restriction of his sampling to one area, few intervals, and one lithology and set of environments.

5) Ellison reduced the number of platform taxa in the Pennsylvanian by about two-thirds. His criteria for placing forms in synonymy were entirely morphologic, and although these groups can be recognized using his definitions, it has become increasingly clear that they are not the most logical possible groupings. For example, the generic grouping of *Idiognathodus-Streptognathodus* must undergo revision based on the phylogeny of the group rather than simply being classified according to the morphology of individuals.

Although the degree of overlap between Ellison's collections in the Desmoinesian and the Allegheny material is small (see sections on ZONATION and INTERREGIONAL CORRELATIONS), several of his conclusions regarding the distribution of genera and species have bearing

Figure 2. Generalized Allegheny columnar section.

Columnar Section



on the present study:

- 1) Desmoinesian faunas are dominated by *Idiognathodus*.
- 2) *Streptognathodus* is "poorly represented" in the Desmoinesian.
- 3) *Gnathodus* is present in the Desmoinesian, but does not

range higher.

- 4) *Gondolella* first appears in the Desmoinesian.
- 5) *Cavusgnathus lautus* is not present in the Desmoinesian.

The first three of his conclusions are substantiated by the Allegheny collections, and on the fourth I have no information. The fifth conclusion is demonstrably incorrect, both for the Appalachians and the Midcontinent.

S T R A T I G R A P H Y O F A L L E G H E N Y
M A R I N E B E D S

GENERAL

Seven marine units have been recognized and named in the Allegheny Group in eastern Ohio and adjacent states. They are commonly listed in the following presumed ascending order: Putnam Hill, Zaleski, Vanport, Columbiana (formerly called Hamden), Tuscarawas, Washingtonville, and Dorr Run Members (fig. 2). The Zaleski can be shown to be the shoreward extension of the Putnam Hill (Cavaroc and Ferm, 1968). The Tuscarawas is at best a brackish, not marine, unit, and of limited areal extent. The Dorr Run is also mostly brackish and contains conodonts (Sturgeon and Merrill, 1949, p. 10), but they are uncommon in occurrence, poorly preserved, and represented by only a single specimen in the collections at hand. The remaining four units, Putnam Hill, Vanport, Columbiana, and Washingtonville have all produced enough conodonts to warrant detailed discussion.

Plates 10 through 13 are basically maps of the localities sampled for Putnam Hill through Washingtonville, respectively. Each map classifies the faunas of the individual localities into Appalachian and Midcontinent provincial faunas (actually Appalachian and mixed) as well as into nearshore (*Cavusgnathus*-biofacies) and offshore examples of the two provincial faunas. Each map also has accompanying stratigraphic sections for each productive locality which present the same faunal analysis in the third dimension.

PUTNAM HILL MEMBER

The Putnam Hill Member usually occurs above the Brookville (#4) Coal which forms the base of the Allegheny Group (fig. 2). Including the Zaleski Flint lithofacies, the Putnam Hill can be traced from the area around McArthur in Vinton County, to the Canton area in Stark County (pl. 10). The thickness and lithology of the unit over most of its outcrop are rather constant, especially so from around Zanesville in Muskingum County northward to Stark County. It is rarely more than a few (commonly not more than two) feet of limestone with 1 to 15 feet of marine shale above. The limestone is a medium bluish-gray which weathers yellow and contains many small fossils which give the rock a distinctive mottled appearance. The fauna is largely molluscan and bryozoan with many incrusting Foraminifera. Over much of the area clay is present in the limestone making it thin-bedded and shaly. Near the northern extremity of its outcrop, the Putnam Hill thickens to ten or more feet of nearly pure limestone. South of Zanesville, the Putnam Hill is mostly calcareous shale, and apparently represents a nearer shore facies. Most lithologic variations are gradual and regional in scale, suggesting that they are the products of a single transgression within a single basin. Within such a transgression, little range in age may be expected from place to place.

VANPORT MEMBER

The Vanport Member is in reality two distinct stratigraphic units, not presently connected, and apparently formed at somewhat different times. For convenience these are referred to simply as

"northern" and "southern" Vanport, separated by an area where marine rocks and faunas are absent (pl. 11). The "southern" Vanport is dominantly a single limestone unit composed of pure, light gray to light buff, hematite stained, sparse fusulinid-*Composita* biomicrite of Folk's classification. Overall, it has low faunal diversity. Compared with the Putnam Hill its thickness is extremely variable, ranging from 0 to 15 feet in thickness within short distances. The "southern" Vanport Limestone is replaced to the north by a mixture of dark gray shale and limestone in northern Vinton County and to the south by shale and siderite in the vicinity of Ashland, Kentucky. Between northern Vinton County and just north of Zanesville (pl. 11), the Vanport Member is missing. Between Zanesville and the general vicinity of Youngstown, the Vanport consists of a mixture of chert and limestone in widely varying proportions and thicknesses (0-20 feet). Commonly these variations occur within a lateral distance of a few hundred yards. The limestones and some associated shales produce small conodont faunas. From Youngstown southeastward into Pennsylvania, the Vanport consists of a single huge wedge of nearly pure limestone up to 25 feet thick and roughly twenty miles wide. Along the southern boundary of these thick limestones and nearer the probable shoreline are thinner limestones, darker in color, with associated dark shales.

AGE RELATIONSHIPS WITHIN THE VANPORT MEMBER

Pure limestone of both the "northern" and "southern" Vanport Member has produced abundant and commonly beautifully preserved conodont faunas. Examination of this material suggests that, although

the age difference is much less than that between either Vanport and the over- or underlying marine units, there are subtle differences (see ZONATION) which indicate that the southern Vanport is somewhat older than the northern Vanport. Their stratigraphic positions are similar and the faunal differences are not sufficient to separate them into distinct biostratigraphic zones. Other aspects of the conodont populations (see PROVINCIAL FAUNAS) support the notion that these transgressions were indeed separated not only in time, but in space, to the extent of having different sources as well.

RELATIONSHIPS BETWEEN PUTNAM HILL AND VANPORT MEMBERS

In northern Ohio there is some ambiguity about the relationships between the Vanport and Putnam Hill Members. Zimmerman (1966, fig. 7) has suggested that the Vanport and Putnam Hill Limestones of Stark County coalesce eastward to form the thick northeastern Vanport Limestone in the Youngstown area. This opinion is not supported by the conodont evidence. Beginning in central Tuscarawas County, the shale interval separating the Putnam Hill and "northern" Vanport Members (Lower Clarion Shale of Zimmerman, 1966) is entirely marine throughout its 20 to 30 feet of thickness. Eastward from here, in the Canton area, the Vanport remains thick, often ten feet or more, and the Putnam Hill increases to a similar thickness at the expense of the intervening shale. In the Canton vicinity, there is neither field evidence nor conodont recovery to indicate that the entire shale interval is marine, although marine fossils can be found some distance above the Putnam Hill Limestone. At the most easterly locality where distinct and discrete Putnam Hill Limestone can be

recognized east of Canton, the Putnam Hill Limestone has thinned to a more normal thickness, but marine fossils are found more than half way up to the Vanport. What happens farther to the east is conjectural. Zimmerman's conclusion is questionable for two reasons. First, from the Tuscarawas County area the total interval can nowhere be demonstrated to be marine. Secondly, along the entire outcrop the conodont faunas of the two limestones can readily be distinguished. A Putnam Hill fauna distinct from that of the Vanport is found even where the interval between them is all marine (and the intervening shales contain intermediate faunas). Near Canton and on to Alliance farther east, the same fauna characterizes the Putnam Hill. The thick northeastern Vanport, on the other hand, contains a fauna which is distinctly Vanport in all respects, even to the base of the unit. There is no evidence of any Putnam Hill equivalent in the base of the thick northeastern Vanport Limestone. As pointed out previously, this northern Vanport fauna is younger than that of the southern Vanport, which in turn *overlies* the southern extremity of the Putnam Hill Member (the Zaleski Flint). The only alternative to Zimmerman's concept is an easterly pinch-out of the Putnam Hill.

COLUMBIANA (HAMDEN) MEMBER

The third widespread marine member of the Allegheny is the Columbiana Member. Its usual stratigraphic position is within a few feet of the top of the Lower Kittanning (#5) Coal. The Columbiana crops out only in the northern half of the area (pl. 12), generally from the vicinity of Zanesville northward. As such, it represents the deposits of a single marine basin, but the lateral variation of

individual rock types is much greater than for the Putnam Hill. Shale is the dominant lithology, but carbonates are present as varying amounts of calcite-siderite nodules. In a few small areas bedded limestones up to two or three feet in thickness occur directly on top of the Lower Kittanning Coal.

WASHINGTONVILLE MEMBER

The highest persistent marine unit of the Allegheny is the Washingtonville Member, which normally occurs directly above the Middle Kittanning (#6) Coal. Its distribution very closely parallels that of the Columbiana Member; however the Washingtonville contains less carbonate than the Columbiana or any of the other major Allegheny marine units. Bedded limestones are almost unknown and the dominant shale lithology is often non-calcareous. The areas where normal marine faunas are most abundant are clustered in the Coshocton County area and along the Ohio-Pennsylvania state line.

DEPOSITIONAL CONDITIONS AND
LITHOFACIES OF ALLEGHENY
MARINE UNITS

INTRODUCTION

In almost any thick vertical section of Allegheny rocks some few thin beds contain marine fossils and these alternate with thicker parts of the section in which marine fossils are absent. The conclusion derived from these occurrences is that marine and non-marine conditions alternated through time at any given location. The marine beds of the Allegheny must therefore represent a series of marine transgressions and regressions in which a set of marine, marginal, and non-marine environments migrated alternately seaward and landward in the sense used by Krumbein and Sloss (1963, p. 311, 312) to define transgression and regression.

Evidence for the migration of the environments and, in what order they succeeded one another through time, is provided not only by the physical characteristics of the rocks, but also by their biologic content. More than merely testifying to environmental changes which occurred at a place through time, the rocks and fossils should also provide an additional record of *why* these changes took place at all, and of the mechanisms which brought them about.

THE MODEL

During the past several years, a model has been developed by Ferm (Ferm and Williams, 1963) and his students to explain the genesis of the Allegheny rocks. Details of this model can be found in Webb, 1963; Flores, 1966; and Zimmerman, 1966. Based on this model, most

of the Pennsylvanian rocks of the Appalachians are detrital in character, deltaic in origin, and fresh water to brackish in habitat. These are predominantly shales and siltstones, but massive sandstones locally attain great thicknesses. The only significant amounts of chemical/biochemical rock occur in clay-coal-limestone packages which form a closely associated and intimately related set of lithosomes.

Active progradation of deltaic wedges caused the accumulation of the large masses of terrigenous sediment. The wedges themselves, by their rapid sedimentation and accumulation, actually triggered the subsequent marine invasion at the same site. Such deltaic masses maintain equilibrium at or near sea level, but if this rapid influx of sediment ceases, generally by diversion of the stream to other areas, the compacting and subsiding mass of sediment stagnates, founders, and is inundated. During this decay, the type of sedimentation passes from dominantly detrital to dominantly chemical/biochemical. Thus in a vertical section, the sediments change from muds and silts of the active delta, through altered clays which probably represent the leached soil profile, into the near sea level organic debris which form coal seams, and finally into marine muds formed as the deltaic lobe was completely inundated. No mechanism other than continuing sedimentation with some slight regional subsidence is necessary to explain the alternation of marine and non-marine beds in such a deltaic complex. For the Appalachian Pennsylvanian, the environment seaward of these progradational deltaic masses was dominantly one of carbonate deposition.

ENVIRONMENTAL AND TEMPORAL SIGNIFICANCE OF TRANSGRESSIONS

The fact that marine and non-marine beds alternate in the Allegheny means that each marine episode began with a transgression and at some point ended with a "regression". The boundary of the transgression is usually fairly easy to pinpoint, especially where marine beds directly overlie coal seams. That the coal-forming plants may well have been brackish in habitat cannot be argued, nevertheless, they illustrate a tie with the land that makes them, for all practical purposes, a part of the continental biota. Further subsidence of these swamps, probably because of continued compaction of the underlying sediments, possibly because of general, regional subsidence, permitted marine transgression.

Because the Allegheny sediments were delta/coastal plain associates, probably more of them were marine in origin than is generally recognized. The absence of marine fossils is not in itself conclusive. Like other transgressive deposits, the bases of these marine beds cannot possibly represent time planes. They do, however, as far as they can be traced laterally, appear to delineate the fairly narrow time span of the transgression. Experience with the modern Mississippi delta shows that a stagnant deltaic mass subsides quite rapidly and marine basins of the size involved in the Allegheny could subside within the order of a few hundred to several thousand years. Because of this, the bases of the marine beds form the nearest thing to a true time datum that we are ever likely to have over any sizeable area in these rocks. It is not too difficult to imagine this transgression proceeding rapidly enough to prohibit the establishment

of well-defined, stable environments. At some point in both time and space, however, each transgression must reach its high-water mark or "still-stand". Whether such a shore line ever stands still for any appreciable length of time is debatable, but given a geologically rapid transgression, it represents the earliest opportunity for real stabilization of environments. Such stable shore lines, representing the limits of the marine basin, are thought to be related to the conodont biofacies discussed in this study. Their recognition is dependent on mapping the areas where marine rocks are present or absent at a given stratigraphic position. In the "regression" which follows, the idealized shoreline must migrate seaward once more, giving the opportunity for similar conditions of shorelines in a vertical succession.

REGRESSION, DEPTH, THICKNESS, AND RATE OF ACCUMULATION

The word "regression" has become linked with withdrawal of the sea, often by tectonic means. It seems unlikely that tectonism played any rôle in the small scale changes from marine to non-marine environments for the Allegheny deposits. Any tectonism involved probably consisted of slow negative movement which provided the general setting for sedimentary accumulation. Change from sea to land is apparently a result of purely sedimentary processes and slower than the reverse change from land to sea. Resumption of active progradation by the lateral migration of a deltaic lobe was the usual stimulus for a "regression", which meant a cessation of one of the two requisites for marine conditions. At this point it seems relevant to mention that the marine environment has two important requirements: first, it is below sea level and aqueous; second, it is of approximately

"normal" salinity. By removing either of these requirements, marine beds are replaced by non-marine ones and a "regression" has taken place. A marine basin may remain normally saline during its filling until it is entirely filled to sea level and choked with sediment. On the other hand, an influx of fresh water may so lower its salinity that it ceases to be marine with little or no increase in the amount of sediment being contributed. The two can, and commonly do, occur concurrently. The nature of the change recorded in the rocks for each of the types may be quite different, however, and it is well worth asking which mechanism was at work to end each marine phase. Do marine fossils disappear upward in a section as the result of filling to or above sea level, or does their disappearance merely signify that the approaching sediment mass, still some distance away, brought enough water of reduced salinity to make their location uninhabitable? With many groups of marine invertebrates this may be difficult to evaluate. Nektonic organisms are less affected by changes in water depth than are associated benthonic ones. Absolute depth of water is not likely to have been a major factor controlling conodont distribution, as these fossils are generally considered to be the remains of nektonic organisms. Changes in salinity, on the other hand, impose as severe a limitation on the nektonic as they would on the benthonic organisms, although the former may be more capable of moving away from the affected area. In the thicker marine intervals in the Allegheny, variations in conodont abundance and population composition suggest that there were areas where each of these mechanisms modified the marine environment at different times. The biofacies herein referred to as "nearshore", probably in fact, reflects reduced salinities. That this biofacies

can most commonly be found near what had been a rather well-stabilized strandline, seems well documented from this work. Its dependence on salinity rather than on depth or some other factor(s), however, is only one possible conclusion, albeit, the most reasonable one under the circumstances. The sedimentary situation on the other hand, involves a general reduction in all faunal elements (with little or no taxonomic change) in terms of numbers of specimens per weight/volume of rock, commonly with some increase in the grain size of the sediments themselves. Also common is a reduction in carbonate content and in such authigenic minerals as pyrite. The conodont fauna in this situation therefore undergoes a reduction in numbers without taxonomic change. No real reduction in the number of animals inhabiting the area actually took place; their remains are as common as ever, simply diluted with an increased volume of terrigenous material. The basin-filling regressive phase of the sedimentary and environmental couplet was probably slower, or at least more irregular, hence less time indicative, than the preceding transgression.

The maximum depths of these marine basins were probably not very great. The thickness of sediment which formed under the most quiet conditions is likewise difficult to estimate, partially because of the extreme compaction (up to 90% for some muds) during diagenesis. This factor also contributes to the uncertainty regarding depth of the basin. The rate of sedimentary accumulation is even more difficult to assess. The duration of most of the Allegheny marine invasions certainly must have been of a magnitude measured in hundreds, if not thousands or tens of thousands, of years. This opinion is at variance

with the work of Zangerl and Richardson (1963) who concluded that the $1\frac{1}{2}$ foot thick shale they studied in the Pennsylvanian of Indiana was deposited in $4\frac{1}{2}$ years. If the longer duration is correct for the Allegheny marine deposits, sedimentary accumulation must have been quite slow. Yet the marine portion of the Allegheny may, in the main, have taken less time to form than the average for the unit as a whole. This conclusion is based largely on the observation that rocks in the Midcontinent region, more largely marine, and taking the same time to be deposited as the Allegheny, are considerably thicker. Because there is no demonstrable, widespread hiatus in the Pennsylvanian of the Appalachians, the overall rate of accumulation must therefore have been slower in the Appalachians than it was in the Midcontinent.

LITHOFACIES PATTERNS

Regional mapping of an Allegheny marine unit illustrates lithofacies roughly paralleling the ancient shoreline (Cavaroc and Ferm, 1968). The most offshore of these is characteristically a limestone lithosome. Shoreward it may grade into either shale or chert, ideally shale followed by chert. Cherts of two genetic types are probably present. One is the thick, diagenetic replacement chert which replaces offshore limestones near their more shoreward limits and is thus not directly related to any of the lithotopes. The second chert type is less common, or at least less significant volumetrically, and represents original deposition of colloidal silica. The Zaleski facies of the Putnam Hill Member probably belongs to this type. Where such chert is absent, the shales grade landward from limey ones associated with the carbonate lithosome, to darker, commonly platy, fissile,

"paper" ones with a reduced, brackish fauna. Therefore, the ideal and complete set of laterally disposed lithofacies, from offshore to onshore, would consist of: marine limestone, marine shale, brackish shale, precipitated chert. Beyond the chert, the last "marine" deposit, the coal formed in the non-inundated part of the swamp, occurs alone. The high level of paleogeographic complexity permitted numerous variations from this simple pattern. Some limestones are probably more shoal deposits while terrigenous muds were deposited farther seaward. In principle the lateral succession of lithotypes should be repeated vertically, but this seldom occurs with any degree of completeness. With the qualification that most marine limestones are succeeded upward by some thickness of marine shale, commonly with a dropout of fauna upward, this vertical repetition does not occur.

GROUPS OF ASSOCIATED CONODONT TAXA

There exists in Pennsylvanian rocks a group of conodont taxa considered by workers since Ellison's 1941 study to be *the* Pennsylvanian conodont fauna. My work on Conemaugh and Allegheny faunas has shown that, although some of the genera and species Ellison listed as most common in the Midcontinent are also common in the Appalachians, other forms he cited are rare or even absent. Conversely, the Appalachian collections contain genera and species seldom or never described from other areas.

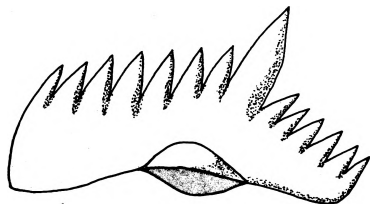
Still other taxa seem to reflect local changes unrelated to these differences between "Appalachian" and "Midcontinent" faunas. Marked increase in the abundance of these other forms indicates environmental control.

A final group of forms seems to be relatively little influenced by these faunal variations, and is, or appears to be, represented everywhere.

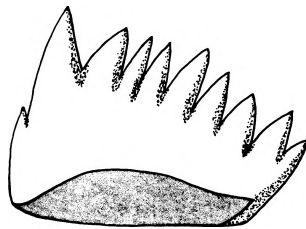
Thus, prior knowledge gained from work with the Conemaugh permitted placing the Allegheny conodonts into four groups of taxa: ubiquitous, Appalachian, Midcontinent, and nearshore biofacies. These groups were used to formulate a working hypothesis to test the significance of their mutual occurrences.

Figure 3. Ubiquitous Allegheny conodonts.

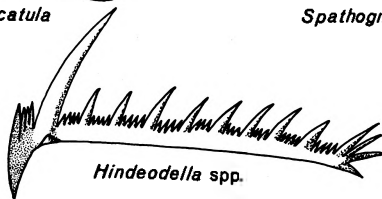
UBIQUITOUS FORMS



Ozarkodina delicatula



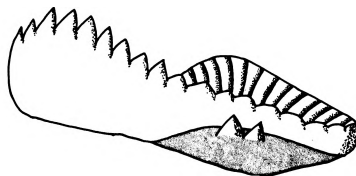
Spathognathodus minutus



Hindeodella spp.



Idiognathodus spp.



Gnathodus spp.

GROUP I

UBIQUITOUS FORMS (fig. 3)

Gnathodus spp.*Idiognathodus* spp.*Streptognathodus* spp.*Ozarkodina* spp.*Spathognathodus* spp.

Others

Most, and usually all, of these forms are present in every Pennsylvanian sample coinciding with the ranges of the individual genera and species. This has proved without exception for every sample from a marine bed from the Allegheny Group. In this context and with the minor reservations that the frame of reference includes only marine Allegheny rocks, these taxa are truly ubiquitous, and conform to both the definition (denotation) and conotation of the word. Exceptions to this rule in non-Allegheny Pennsylvanian rocks are known to occur, but are sufficiently rare to recommend the retention of this term and its extension to other areas and units.

GROUP II

"APPALACHIAN" PROVINCIAL FORMS (fig. 4)

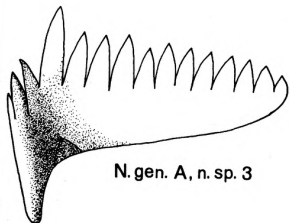
Hibbardella n.sp. 2*Hindeodus* spp.*Ligonodina* n.sp. 4*Neoprioniodus* n.sp. 7

New genus A, n.sp. 3

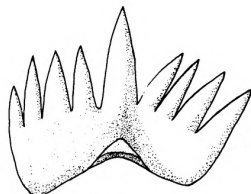
New genus B, n.sp. 1

Figure 4. Appalachian provincial conodonts.

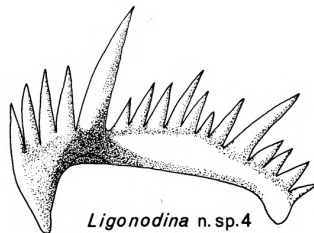
APPALACHIAN FORMS



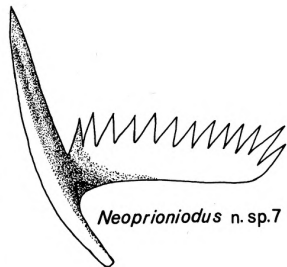
N.gen. A, n. sp. 3



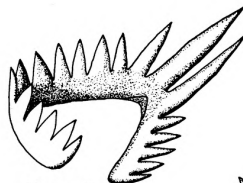
Hindeodus n. spp.



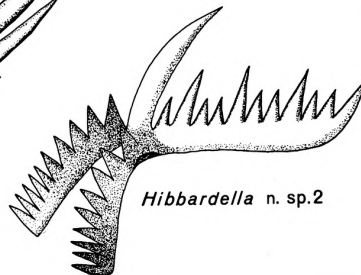
Ligonodina n. sp.4



Neoprioniodus n. sp.7



N. gen.B, n. sp.1



Hibbardella n. sp.2

Like Groups III and IV, this group can only be a part of the fauna, requiring support from the "ubiquitous" group, and consequently never occurs alone.

GROUP III

"MIDCONTINENT" PROVINCIAL FORMS (fig. 5)

Hibbardella subacoda (Gunnell)

Ligonodina lexingtonensis (Gunnell)

Ligonodina typa (Gunnell)

Lonchodina spp.

Metalonchodina spp.

Neoprioniodus spp., except n.spp. 7 and 10

Gondolella is omitted from the above list because it has not been found in the Appalachians. It is perhaps the most characteristic (and most restricted) member of the Midcontinent fauna.

GROUP IV

CAVUSGNATHUS-BIOFACIES (fig. 6)

Cavusgnathus spp.

Hibbardella n.spp. 1 and 3

Ligonodina n.sp. 10

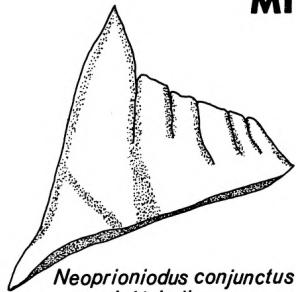
Neoprioniodus n.sp. 10

With the addition of a few of the ubiquitous forms (*Ozarkodina*, *Spathognathodus*, *Hindeodella*) representatives of this biofacies can approach the total fauna. Such a situation is rare, but has been observed, although never in the Allegheny.

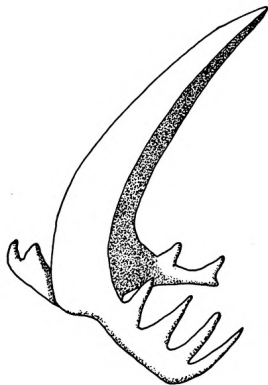
Three Pennsylvanian platform conodont genera are through going and ubiquitous, *Gnathodus*, *Idiognathodus*, and *Streptognathodus*. A

Figure 5. Midcontinent provincial conodonts.

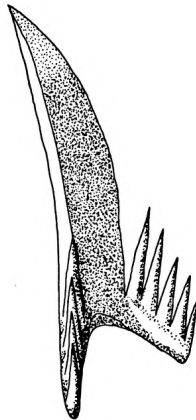
MIDCONTINENT FORMS



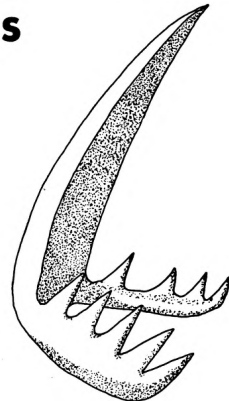
Neoprioniodus conjunctus
+ *N. bulbosus*



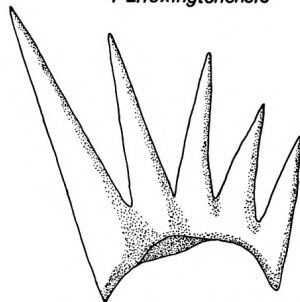
Hibbardella subacoda



Lonchodina clarki
+ *L. ponderosa*



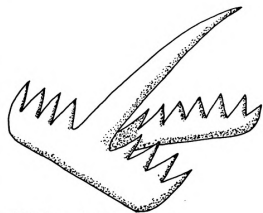
Ligonodina typa
+ *L. lexingtonensis*



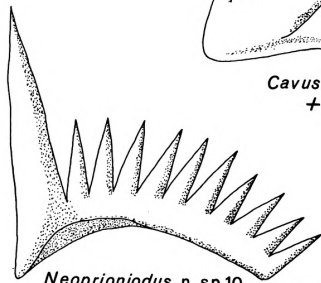
Metalonchodina bidentata

Figure 6. *Cavusgnathus*-biofacies conodonts.

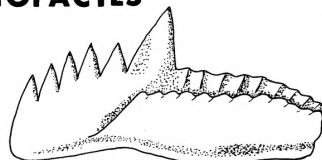
CAVUSGNATHUS BIOFACIES



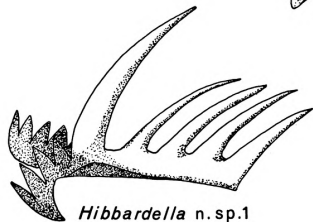
Hibbardella n.sp.3



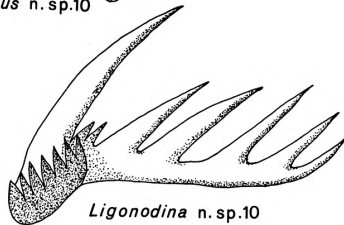
Neoprioniodus n.sp.10



Cavusgnathus gigantus
+ *C. lautus*



Hibbardella n.sp.1



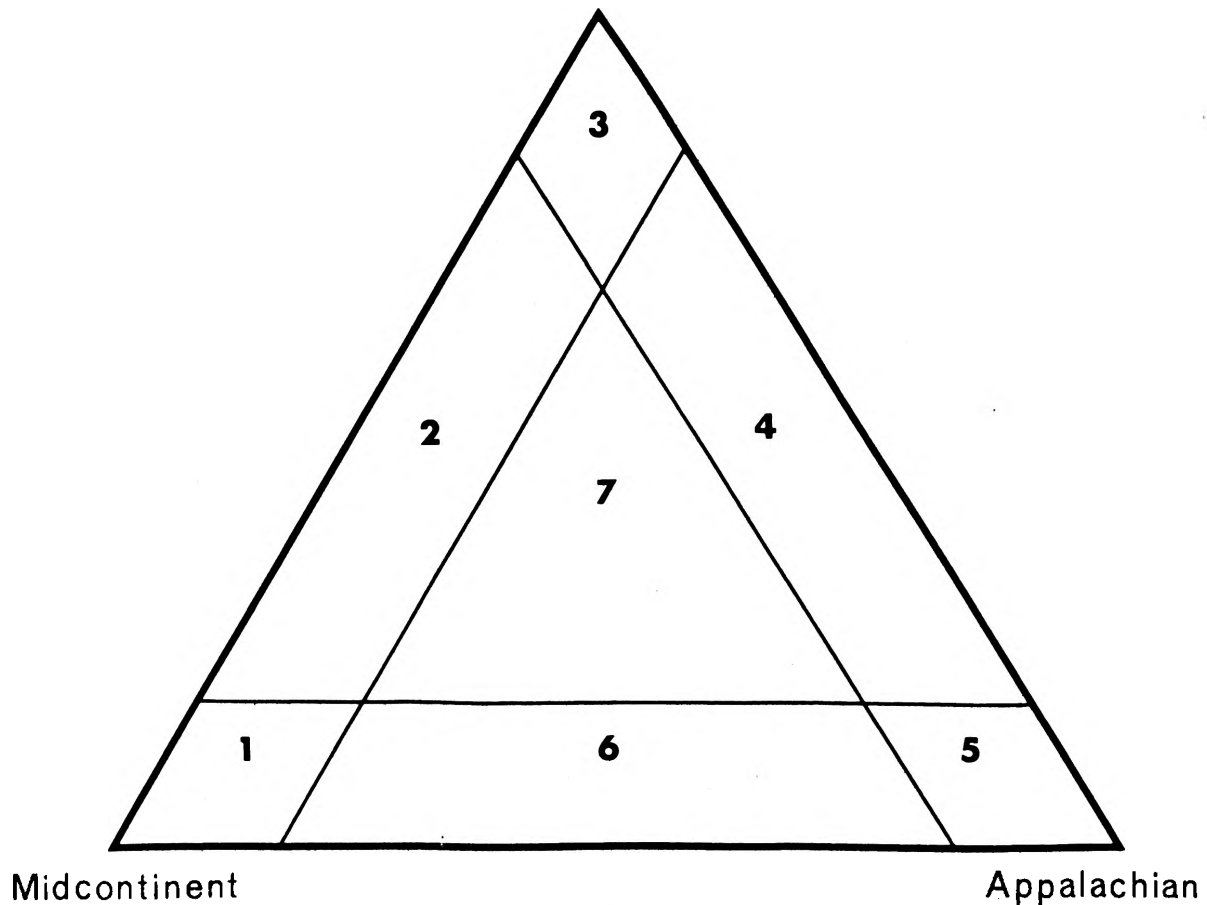
Ligonodina n.sp.10

fourth, *Cavusgnathus*, is environmentally restricted. *Gondolella*, the fifth and last platform genus of this age, has not been found in the Appalachian region and probably represents the most restricted taxon of the Midcontinent fauna. A definition and discussion of the meaning of platform conodonts has been well stated by Lindström (1964, p. 91-107).

Figure 7. Triangular diagram illustrating possible and observed combinations of non-ubiquitous taxa.

Mutual Occurrences of Conodont Groups

Cavusgnathus-biofacies



1. Nearly all described faunas from the Midcontinent.
2. Not certainly known, probably occurs in the Midcontinent.
3. Ames Member (Conemaugh) in southernmost Ohio.
4. Nearshore facies of Conemaugh units, southern Vanport, Columbiana, and Washingtonville.
5. Offshore facies of nearly all Appalachian units, in the Allegheny, the Southern Vanport, Columbiana, and Washingtonville.
6. Offshore facies of Northern Vanport and Putnam Hill.
7. Nearshore facies of Northern Vanport, and Putnam Hill.

CONODONT BIOFACIES

HISTORICAL VIEWPOINTS

Recognition of temporally equivalent biofacies depends heavily upon identification of the deposits as synchronous, as well as observation that their contained faunas are unlike. Earliest conodont workers, from 75 to 100 years ago, either had no evidence for faunal differences or reached no conclusions about the environmental significance of the conodont remains they studied. At a somewhat later date, just before and following the turn of the century, the easily observed occurrences of conodonts in black shales led paleontologists to the belief that, as a group, the conodontophores were restricted to "the black shale environment".

Our increasing knowledge has caused us to realize that conodonts are most abundant, for sedimentary rather than biologic reasons, in limestones, and that the black shales are among the poorest rocks for conodont study, in terms of both abundance and preservation.

More recent thought seems to favor the proposition that no differences exist between synchronous conodont-bearing deposits in their taxonomic composition or faunal diversity, but only in the frequency of specimens in different rock types. Lindström (1964, p. 66, 67) discusses "facies", but only cites examples of this latter sort. He does not consider the biofacies in which differing taxa are found in synchronous deposits. Müller (1962, p. W89) is even more explicit in denying taxonomic differences attributable to environmental control. These two references are representative of the thinking of most conodont workers today and a fair summary of their statements both

public and private.

References citing significant taxonomic differences between conodont faunas of equivalent age do exist, but are relatively uncommon. Not all of these are biofacies; Sweet and Bergström (1962) summarized differences observed between Ordovician faunas from Europe and North America that appear to be provincial rather than environmental in origin. More recently Bergström and Sweet (1966) have described subtle differences contained in samples within a single Ordovician locality that probably reflect conodont biofacies. Globensky (1967) noted local variations in his faunas which he believed to be related somehow to tectonism. Davis (1967) recorded different ratios between two well known Devonian platform genera (*Polygnathus* and *Icriodus*) with variation in the amount of terrigenous influx.

Rexroad (1958) described a "southern faunal province" in the Glen Dean (Chesterian, Mississippian) in the Illinois Basin. A species of *Cavusgnathus* is involved in distinguishing between "provinces", but is not abundantly represented (total of 71 specimens); although it occurs at all but 3 of his 17 localities. It is only common at 2 localities and these two localities constitute the "southern faunal province" concept as elaborated by Rexroad and Jarrell (1961). In their study, three Chesterian units were evaluated, largely on the basis of their ratios between the platform genera *Gnathodus* and *Cavusgnathus*. No counts of total specimens were given, but from the frequencies per kilogram it is obvious that the middle unit of the three (Fraileys Formation) was least productive and probably that the total material involved consisted of several hundred specimens. The

contrast between the upper (Haney) and lower (Beech Creek) formations is striking. *Cavusgnathus* : *Gnathodus* generic ratios for the Haney average 34:1 and for the Beech Creek Formation, 1:6. Rexroad and Jarrell attribute these differences to provincialism rather than biofacies; a conclusion inconsistent with comparable situations found in the Pennsylvanian. However, theirs is a valuable, parallel set of occurrences, and illustrates variations involving some of the same taxa.

At almost the same time Rexroad and Jarrell published their paper, an abstract (Merrill, 1962) announced similarly different proportions between *Cavusgnathus* and *Streptognathodus* in the Conemaugh Group. These differences were attributed to environment rather than province. Later works added more information (Merrill, 1964, 1966, 1967) about the same and similar occurrences. Credit for the discovery and, in my opinion the correct interpretation, of this kind of variation in the Pennsylvanian between *Cavusgnathus* and *Streptognathodus* belongs to Drake (1958), although the full implications of his discovery may not have occurred to him.

ALLEGHENY EVIDENCE FOR CONODONT BIOFACIES

Regional patterns of faunal variations within each unit provide complimentary evidence to the even more unequivocal testimony provided by differences within single outcrops. These gross patterns of large concentrations of *Cavusgnathus* and its associated taxa roughly coincide with or at least closely parallel the ancient shore-lines as mapped by the limits of marine deposits. Volumetrically, the nearshore- or *Cavusgnathus*-biofacies beds are most abundant in the Vanport Member, although the biofacies is present in each of the other

productive Allegheny marine units, at least locally. The evidence for these conclusions can be derived from the counts of specimens from each sample (in pocket) and are summarized on the maps for each unit (pls. 10-13).

REGIONAL PATTERNS

Putnam Hill occurrences.- The high concentrations of the *Cavusgnathus*-biofacies in the Putnam Hill Member are clustered in the area near Zanesville, mostly in Perry and Muskingum Counties. This area is close to the southern shoreline of the main Putnam Hill depositional basin (pl. 10) and corresponds closely also to the limit of limestone deposition within the basin.

Vanport occurrences.-Not only are the Vanport occurrences (pl. 11) of the *Cavusgnathus*-biofacies the most widespread, they also offer the best evidence for the spatial relationships between this biofacies and the one dominated by *Idiognathodus*. In the southern Vanport basin, the massive limestone contains moderate numbers of the *Cavusgnathus*-biofacies, indicating an overall influence of these nearer shore elements, and a roughly symmetrical distribution from south to north corresponding to distance from shore. Near the southwestern extremity of the basin a poorly fossiliferous shale at locality 16 produced a single specimen of *Cavusgnathus*, and no other platform conodonts. Such a sparse collection can no more than suggest the composition of the living population and the fact that it was a specimen of *Cavusgnathus* may be no more than coincidence. The southernmost samples of massive limestone (loc. 15) produced ratios of *Cavusgnathus* to total platform elements of 1:4 (see statistical data in

appendix). This ratio decreases in a general way to the north and northeast and in extreme northern Lawrence and southern Jackson Counties may reach 1:9 or less. Exceptions are present, but a crude gradient seems to exist. The northern edge of the basin in Vinton County shows transitions within the limestone in short distances with increases in the numbers of *Cavusgnathus*. However, no ratio greater than 1:3 has been observed in any collection from the pure limestone.

The western part of the northern Vanport is composed of lenticular limestones, cherts and shales. Many samples contain a relatively large proportion of individuals belonging to the *Cavusgnathus*-biofacies. In this connection the northwestern Vanport with its moderate to large numbers of nearshore species is more like the southern Vanport than it is the northern Vanport farther east. In the northwestern Vanport there are localities which are dominated at least in part by the *Cavusgnathus*-biofacies and others where only occasional specimens from it are encountered.

In contrast, the massive, pure, northeastern Vanport Limestone contains a conodont fauna which is strikingly homogeneous in that among over 3,000 specimens, from 30 subsamples taken at 5 different sample/localities (1, 8, 34, 35, 38) not a single specimen of *Cavusgnathus* has been found, and only one specimen of any of the taxa assigned to the nearshore biofacies. This places it solidly in the *Idiognathodus*-biofacies. Its degree of dominance by these offshore forms is illustrated by comparison with the southern Vanport Limestone. With only half as many total specimens, the pure southern Vanport Limestone has produced more than 100 specimens of the nearshore genus *Cavusgnathus* (plus additional specimens of its associates)

despite the fact that it too belongs to the *Idiognathodus*-biofacies. *Cavusgnathus* is present along the southern margin of the northeastern Vanport carbonates in dark shales and thin, shaly limestones at three localities (3, 7, 37).

Columbiana occurrences.-Only one locality (loc. 2) in the Columbiana is dominated by *Cavusgnathus*. At this locality near the southern extremity of the basin (pl. 12), the ratio of *Cavusgnathus* to other platforms is 2:1. Northward, in the main part of the basin, the next few localities have ratios of 1:10 (loc. 4), 1:30 (loc. 5), 1:80 (loc. 7), 1:75 (loc. 9), and 1:300 (loc. 10). At the northernmost Columbiana localities (20 and 21), samples have ratios equalling or surpassing the one at locality 10, establishing that *Cavusgnathus* decreases in abundance northward. No samples from the Columbiana are close to the probable northern shore of the basin.

Washingtonville occurrences.-No gradient can be demonstrated for the Washingtonville similar to that in the other Allegheny units. Like the Columbiana, only a single locality in Muskingum County can truly be said to be dominated by *Cavusgnathus* (pl. 13).

BOTH NEARSHORE AND OFFSHORE BIOFACIES WITHIN SINGLE OUTCROPS

One biofacies, dominated by *Idiognathodus* (with minor numbers of *Streptognathodus* in most units), presumably the more offshore, and another dominated by *Cavusgnathus*, and presumably the more nearshore, alternate repeatedly in the Allegheny. Small scale vertical and lateral concentrations of the elements of each biofacies indicate migration of the shoreline and the parallel suite of environments through time. Theoretically, in every marine transgressive-regressive couplet there should be an alternation upward between nearshore-offshore-nearshore

biofacies. This double transition has not yet been observed, but probably occurs. Several localities illustrate an offshore facies being succeeded upward by the nearshore, and several others the reverse.

The majority of the occurrences of the *Cavusgnathus*-biofacies are present in shales. However, enough of them are in limestones to demonstrate again that lithofacies and conodont biofacies are incongruent. The present interpretation, that this biofacies represents nearer shore and less saline conditions, is consistent with the less calcareous, more detrital nature of most of the rocks containing it. The macrofossil occurrences associated with the *Cavusgnathus*-biofacies are commonly rich in chonetid brachiopods, linguloid brachiopods, and pectenoid bivalves, all forms usually considered as brackish water inhabitants.

The most compelling evidence for biofacies control of the *Cavusgnathus* fauna in a single outcrop is found at Vanport locality 24 in Vinton County where in a single strip mine the southern Vanport is represented by 8 feet of limestone which in less than 200 feet to the south passes into dark shale (fig. 8). On the north side of the road two samples of the pure, massive limestone had ratios, *Cavusgnathus* : all other platforms averaging 1:9. Beneath this limestone is a dark shale, 2 feet thick. Although the lower foot seems to be more dominated by *Cavusgnathus* than the upper, the two average, for two samples from each foot, 9:1, a ratio exactly the reverse of that from the limestone directly in contact above. South of the road, and less than 200 feet away, dark calcareous shale with limestone nodules produces ratios for both averaging 2:1.

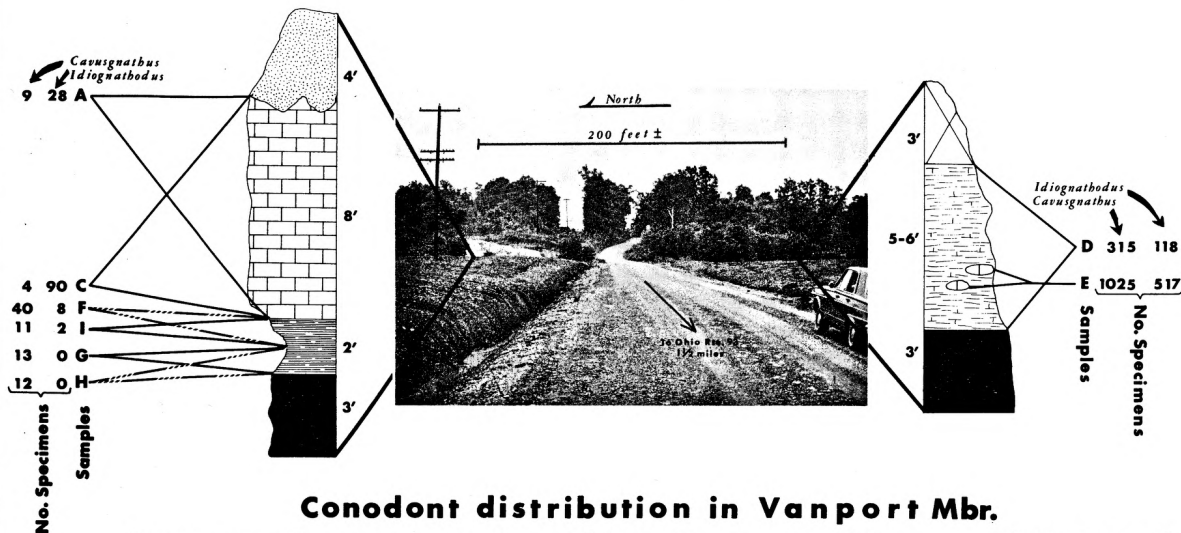
An almost equally striking but similar example is provided by

Figure 8. Conodont distribution at Vanport locality 24.

Section

Location Photograph

Section



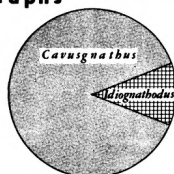
Conodont distribution in Vanport Mbr. at Locality Vanport 24

(see text for location and explanation)

Summary graphs

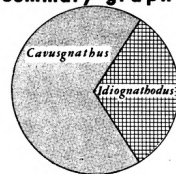


Pure ls.



Dark sh.

Summary graph



Dark sh. & ls.

Vanport localities 4 and 22 some two miles from locality 24. Locality 22 consists of about eight feet of pure limestone (average ratio *Cavusgnathus* : all other platforms = 1:4) overlying two feet of dark gray calcareous shale (ratio 9:1). At this place the initial transgression was high in organic material and dominated by *Cavusgnathus*, in exactly the same manner as the northern part of locality 24. Also like the northern part of locality 24, this dark material was succeeded by a cleaner, less fetid, carbonate lithotope, dominated by *Idiognathodus*. To complete the analogy, less than one-half mile south of locality 22 is locality 4 which is analogous to the southern part of locality 24. Locality 4 consists of dark calcareous shales and thin limestones with numerous chonetid brachiopods. Five samples of these beds all had ratios of 1(+):1(-). With more than 50% *Cavusgnathus*, it certainly belongs to that biofacies, and is closely similar to the beds south of the road at locality 24. In both these examples the shales beneath the pure limestones are the most strongly dominated by *Cavusgnathus*, the overlying limestone is strongly *Idiognathodus*-dominated, and the thick shale - thin limestone lithofacies a short distance south is a mixture of the two, with *Cavusgnathus* still being the leading platform taxon. Because reworking is unlikely for these localities, a meeting and mingling of living animals is the most reasonable answer to these distributions. Figure 8 gives the locations, lithologies, and actual counts of specimens recovered from locality 24. Only the platform genera which are the diagnostic taxa for the two biofacies are listed. Therefore, a few specimens of the closely related *Streptognathodus* are included in *Idiognathodus*, but *Gnathodus*, with no demonstrable close affinity is not included or listed. *Gnathodus* occurs in comparable

proportions in each biofacies, establishing that it was not greatly influenced by the same environmental factors which affected *Cavusgnathus* and the *Idiognathodus-Streptognathodus* lineage. Non-platform elements in the two biofacies conform quite well to the groupings listed under GROUPS OF ASSOCIATED CONODONT TAXA; that is, the abundance of such taxa as *Hibbardella* n.sp. 3 is greatest concomitant with a maximum abundance of *Cavusgnathus*.

Much higher total frequencies in the *Cavusgnathus*-biofacies south of the road at locality 24 and at locality 4 are anomalous and may indicate some concentration of these remains by physical processes. If this was a beach or bar deposit, it was one of extremely low-energy, for there are proportionally as many fragile, easily transported, and easily destroyed forms in the southern parts as in the northern.

Higher percentages of *Cavusgnathus* and its associated taxa in localities such as these present several questions. A most basic one which has not been raised previously in this study involves two mutually exclusive alternative explanations for these concentrations, both environmental, but poles apart in their meanings. They can best be summarized with the question: Does the high concentration of *Cavusgnathus* indicate a more or less hospitable environment for the creatures bearing these elements? They were buried at these places in large numbers, and, for reasons already stated, I believe that they also died there in equally large numbers. There still remains the vexing question as to whether or not their deaths were the *result* of the environment or whether they simply died where they lived in abundance and well adapted to their environment. No answer to this question can be given from the evidence at hand. There is a second question, somewhat

related to the first, which offers more hope of solution: Do the higher frequencies in deposits like those south of the road at locality 24 indicate a genuine decrease in the abundance of *Idiognathodus*-bearing individuals or merely a tremendous influx of those bearing *Cavusgnathus*? Other taxa, especially *Gnathodus*, occur in nearly equal proportions within the the two biofacies. Based on this and similar controls, it appears that the increase in *Cavusgnathus* cannot be explained by mere addition of that genus to a previously *Idiognathodus*-dominated fauna or similar dilution would be observed in control taxa such as *Gnathodus*. A genuine decrease in *Idiognathodus* seems necessary to explain the observed ratios.

These environmentally influenced localities lie along one margin of the mapped southern Vanport marine basin. They do, in fact, partially delimit this ancient shoreline. From the vertical succession of biofacies it can be concluded that, as the sea transgressed, the more brackish rim was inhabited by a pioneer community rich in *Cavusgnathus*-bearing organisms. This pioneer community was succeeded over most of the basin by a community dominated by *Idiognathodus*-bearing organisms, but the succession was not fully realized along the limits of the transgression. Along the shoreline the more brackish environment permitted *Cavusgnathus* to flourish (alternately it killed that genus and some others in the manner of the "red tide"), although its dominance was reduced somewhat by an influx of offshore forms. Presence of only this nearshore facies almost necessitates a relative stability of shoreline. The absence of the usual succession as preserved in the transgressive-regressive couplet at most localities seems best explained by relatively rapidly changing conditions which prohibited the nearshore

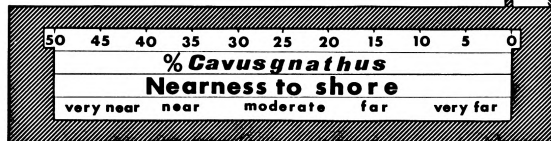
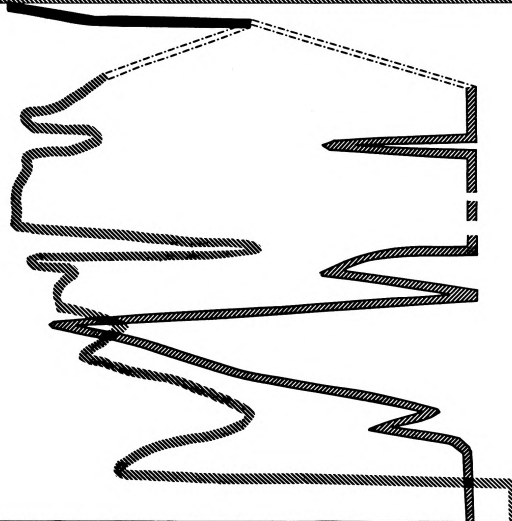
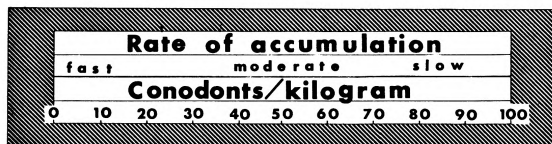
community from becoming well established.

One of the best localities to show coincidence of conodont biofacies, rock type, and macrofauna is Putnam Hill 3/Vanport 3. This totally marine shale separating the Putnam Hill and Vanport Limestones was sampled in one foot intervals and is shown in detail in figure 9. This locality provided an unparalleled opportunity to study all aspects of Allegheny conodont distribution through a considerable thickness of marine rock. Most of the shale between the two limestones has low to very low total conodont frequencies. This in itself becomes a paleo-ecologic tool. The concept that frequency is inversely proportional to the rate of sedimentary accumulation is not new, Lindström (1964, p. 68-71) summarizes it well. It may be a dangerous concept if applied too strictly to relatively small intervals in the manner that I have done. Nevertheless, it is a useful concept, the validity of which seems to be on fairly firm ground. The differences in the frequency of conodonts per kilogram at this locality do indeed seem to describe a definite pattern. A sample from any given interval of this shale may have a conodont frequency ten times as large as from some other interval of comparable size. If the disjunct parts of the conodontophores did fall to the sea bottom like continuous, if gentle, rain, then the interval producing the greater frequency had the slowest rate of lithic fill, in this case, terrigenous mud. Derived from that concept is an even less safe corollary, that the foot interval with the 100 specimens/kilogram took ten times as long to accumulate as another with a frequency of 10/kilogram. The rate of sedimentary accumulation is directly related to the process of basin-filling, and although less than secure, the use of conodont frequencies promises to

Figure 9. Conodont distribution locality Putnam Hill 3/Vanport 3.

Conodont distribution at locality Putnam Hill 3/Vanport 3

(see text for location and explanation)

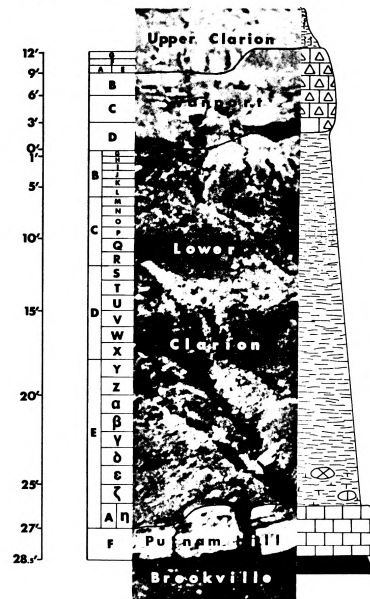


Scale
in feet

Samples

Photography

Lithology



be one tool to estimate the relative rates. The shale of Putnam Hill locality 3/Vanport locality 3, represents the deposit of a marine basin in the process of being filled; but in which the subsidence kept pace with filling, producing an unusual, totally marine, interval. It did not become non-marine by the mechanism of filling as was the usual termination for such marine episodes.

If the concentrations of *Cavusgnathus* are taken as indicators of the other influence which destroys marine environments, freshening by land-derived waters, then it can be seen that the two are not always coincident. Several episodes of salinity reduction and several of an increase in terrigenous influx are recorded, but they only coincide at certain levels. Above the Vanport Limestone and Chert, the rapid drop in frequency, coupled with increase in *Cavusgnathus*, illustrates both agents operating strongly and concurrently. The result is a rapid disappearance of all marine fossils. The basin filled and its salinity was reduced to near fresh water conditions. This marks the end of a marine interval during which sediments now preserved as over forty feet of rock were deposited, the largest such marine thickness found anywhere in the Allegheny Group. Roberts (1966) has outlined closely similar occurrences at this same locality involving macrofossils which seem to reflect changes both in salinity and amount of detrital material. Our data differ only in detail.

PROVINCIAL FAUNAS

Provincialism among conodont faunas has been described from Ordovician rocks by several authors and summarized by Sweet and Bergström (1962) as "Anglo-Scandinavian" and "Midcontinent-American" provinces. No similar occurrences have been described from the middle Paleozoic, but Rexroad (1958) and Rexroad and Jarrel (1961) have noted Late Mississippian faunal provinces, one characteristic of the Illinois Basin, and the other of central Texas. However, these provinces are based primarily on the relative abundance of *Cavusgnathus* which, in the preceding chapter, was shown to be environmentally rather than provincially controlled in Pennsylvanian faunas.

Previous work with Conemaugh faunas (Merrill, 1966) has demonstrated that very few specimens of the non-platform taxa described by earlier writers from rocks of the same age in Kansas, Missouri, and Texas are present in the Conemaugh. This departure from the expected faunal composition is overwhelming and led to the definition of an "Appalachian" and a "Midcontinent" provincial fauna. Allegheny faunas likewise differ from those of the Midcontinent in ways which are neither biostratigraphic nor demonstrably environmental. Like the Ordovician provincial faunas these appear to be geographically oriented, although not entirely restricted. Pennsylvanian examples are like the Ordovician ones also in that both contain some ubiquitous elements, and some elements which are less restricted than others. Another factor, that of mixing of the two faunas in varying proportions, adds to the complexity. The significance is that there are two definable

groups of taxa which can be mutually exclusive and distinguished from the biofacies differences which are also present. Most of the following discussion will be confined to the Allegheny occurrences although the Conemaugh faunas provide more dramatic evidence of provincialism.

The collections from the Putnam Hill Member contain over 1,000 specimens of taxa assigned to the two provincial faunas. No significant differences could be detected between the various localities or between the lithosomes; the Putnam Hill is thus, provincially speaking, homogeneous. The ratio between Appalachian and Midcontinent taxa for this unit is approximately 1:2. Although clearly weighted to the Midcontinent, this is not an overwhelming difference, and consequently this fauna is considered simply to be mixed provincial. Nevertheless, there is a greater concentration of Midcontinent elements in the Putnam Hill than in any other unit so far studied in the Appalachian region.

The Vanport Member, with its regional diversity of lithologies and faunas, as expected, provided the most interesting data. The southern shales and limestones, although strongly contrasting in biofacies, are provincially rather homogeneous, with ratios between Appalachian and Midcontinent forms in the shales and limestones of 40:1 and 15:1, respectively. Although there is some difference in the absolute proportions, possibly through selective preservation, they are both quite uniform in being universally and heavily dominated by Appalachian forms. This preponderance of Appalachian forms is much like that in most collections from samples taken from the overlying Conemaugh Group.

The limestones, cherts, and associated shales of the western part of the northern Vanport appear to have each about equally represented, although only approximately 15 specimens of each fauna have been collected.

The eastern part of the northern Vanport shows, in the limestone, a preponderance of Appalachian forms by a 5:3 ratio. This also approaches a 50-50 mixture, far more mixed than the underlying Putnam Hill. Conversely, the shale margins of the northeastern Vanport, lying along the southern flank of the main limestone mass, have a ratio of about 1:2. Just why this difference in ratios exists between the limestone and shale is not presently known. The collections from the shale are moderately large, but are dominated by a single locality so that they may not be representative. The shale ratio is nearly identical to the one for the Putnam Hill and the entire northeastern Vanport can be considered in a broad sense to be mixed in much the same manner as the Putnam Hill. Summarizing the entire Vanport, the southern area is entirely Appalachian in its affinities and the northern portion contains a mixture of elements from the two provincial faunas.

Columbiana faunas are not as uniform as the underlying units', and a few localities show rather large concentrations of Midcontinent forms, especially toward the center of the basin in Stark County. The margins are dominated by Appalachian taxa, although the gradient is not well-defined and local departures from this simple pattern occur. The overall ratio is in favor of the Appalachian taxa by 5:1, and despite some invasion by Midcontinent elements, the fauna definitely belongs to the Appalachian province.

Washingtonville occurrences are somewhat more homogeneous and more Appalachian in character, the overall ratio being 20:1.

Not all of the Midcontinent taxa have been found in the Appalachians, nor are the ones that are found equally represented. *Gondolella* is the most conspicuous because it has not been found at all, not a single individual among more than 100,000 Pennsylvanian conodont specimens from the Appalachians.

It is more difficult to define which of the other taxa are more restricted than the group as a whole, because all occur in at least some of the samples collected. Of the remainder of the group, *Neoprioniodus conjunctus*, *N. bulbosus*, and *Metalonchodina* spp. seem to occur in fewer samples than the others. *Hibbardella subacoda*, *Ligonodina lexingtonensis*, and *L. typa* seem to be next, and *Lonchodina* spp. the least restricted. With *Lonchodina* there is some doubt because some forms assigned to the genus may actually have Appalachian affinities. At the least, it is a common "line-crosser", as common as *H. subacoda* and the two species of *Ligonodina*.

Tendencies for the individual Appalachian taxa to mix with those from the Midcontinent are difficult to assess because no strongly Midcontinent-dominated faunas have been collected from rocks of the Appalachians to test the restriction of the taxa of that province. The forms which seem to occur most commonly, however, are *Ligonodina* n.sp. 4, New genus A, n.sp. 3, and New genus B, n.sp. 1, but this may simply be because they are less fragile and hence more easily preserved than the remaining forms.

The Pennsylvanian Midcontinent fauna resembles that from the Mississippian Barnett Shale of Texas which was referred to the

"southern faunal province" of Rexroad and Jarrell (1961). Conversely, the taxa of the Appalachian fauna are much more similar in gross morphology to the Illinois Basin forms described by Rexroad *et al.* in several publications. Thus there is a suggestion of origin and ancestry, but no unquestioned proof.

The vertical succession of ratios among the Allegheny units (disregarding for a moment the variations in the Vanport Member) illustrates a continuous trend toward greater domination by Appalachian forms, a trend that continues and is amplified in the overlying Conemaugh Group. This relationship is probably not the result of chance. Reconnaissance collecting in the Midcontinent region shows that the same trend appears to be present there, with progressively fewer units displaying the classic Midcontinent fauna upward through the column and higher units become more and more "Appalachian" in aspect. Exactly the same taxa mutually occur that were predicted by the Appalachian region associations. This is heartening from the standpoint of helping to establish differences in contemporaneous conodont faunas. The Midcontinent region samples are disquieting in one respect, the "provincial" faunas commonly succeed one another through such short vertical distances as to suggest environmental rather than provincial control. Thus, the differences I am ascribing to provincialism eventually may prove simply another pair of biofacies; although, presumably, of a sort distinct from the one already documented. At present these variations are best explained through provincialism for the Allegheny Group.

PLATFORM PHYLOGENIES , ZONATION , AND INTERREGIONAL CORRELATIONS

PHYLOGENIES AND ABUNDANCE

Of all conodont genera, the platform kinds show the greatest complexity, and most rapid evolutionary change. They are thus very suitable for biostratigraphic zonation. The very nature of platform complexity, rapidly changing morphology, and the modification of diverse non-platform types into platforms, while providing bountiful tools for biostratigraphy, simultaneously produces an almost inevitable by-product of the evolution of a great many similar forms; homeomorphy is common. The degree of homeomorphy is not uniform; some examples are virtually identical, others only show gross similarity. Homeomorphy presents a pitfall to anyone pursuing a purely morphological, typological approach to conodont taxonomy and conodont workers have made considerable progress in avoiding this pitfall by studying populations phylogenetically and phylomorphogenetically rather than adhering to rigid definitions of morphospecies.

It is worthwhile to present a discussion of the phylogenies of the Allegheny platform genera outside the chapter on systematics because these phylogenies form the basis on which practical biostratigraphic subdivisions must be founded. It is not possible to exclude all systematic elaboration and interpretation from the resulting discussion, but an effort is made to reduce this overlap.

Cavusgnathus.—The oldest cavusgnathids are found in Middle Mississippian rocks. A transition from *Taphrognathus* to *Cavusgnathus* has been demonstrated, but the ancestry of the former genus

has not been established. Several closely related species of *Cavusgnathus* are found at different levels through the remainder of the Mississippian. Forms similar to some of these cavusgnathids have been found in the oldest Pennsylvanian rocks so far studied, and the genetic continuity across the systemic boundary seems highly probable. The changes which took place near this boundary were important and the problems peculiar. They will be discussed more fully in the systematics of the genus. There is presently no evidence, other than inferences made from published reports when compared with Pennsylvanian observations, that *Cavusgnathus* was environmentally restricted during the Mississippian, but in the oldest Pottsville rocks its occurrence does seem to be related to environment. Therefore, an important change in its distribution and mode of life may have taken place sometime near the beginning of the Pennsylvanian. The genus ranges upward for an undetermined distance into Permian rocks. Its history from the oldest Pennsylvanian occurrences to the end of its known range is one of remarkable uniformity. Evolutionary changes were slow or in most cases non-existent.

Several morphologic developments recur within the genus. For example, Mississippian species usually possess a well-defined fixed blade. Most Pennsylvanian forms do not show this, although there is some latitude in the development of this feature. Some Mississippian forms may not have a fixed blade as in the lineage to "*Streptognathodus unicornis*" of Rexroad and Burton, and therefore are like the majority of Pennsylvanian forms. The usual eccentric position of the blade, attached to the outer margin of the platform, is not invariable, and a more central location is found not only in the lineage leading to "*Streptognathodus unicornis*", but again

in *C. flexus* and related forms in the Upper Pennsylvanian.

All Mississippian forms with eccentrically positioned blades are dextral specimens. The genus as a whole in the Mississippian is right-sided or "right-handed". In the Pennsylvanian both right and left "handed" forms are present, *C. laetus* is the left or sinistral species and *C. gigantus* the right or dextral form, at least in the Allegheny rocks where they are the only two species present. Furthermore, in any given sample the ratio between the two "species" invariably approaches 1:1, suggesting that they are the symmetrically paired elements from the body of the same natural species. However, their ranges may not prove to be entirely coincident and other species, for example, *C. flexus*, complicate the picture in younger rocks. A further treatment of the significance of this symmetry will be given in the systematics. A few specimens of both the Allegheny species from all stratigraphic levels possess enlarged denticle-like nodes at the posterior junction of the parapets, but this feature is both uncommon and seemingly unimportant; although it is apparently less common in younger beds.

Gnathodus.—A particular quotation seems *à propos* to characterize the changes in morphology of this genus in Pottsville and Allegheny rocks:

*"All right", said the Cat; and this
time it vanished quite slowly, beginning
with the end of the tail....*

(Dodgson, 1904, p. 88).

The oldest forms assigned to this genus are found in youngest Devonian rocks in both Europe and North America and became abundant in the Mississippian.

A very serious problem is encountered in crossing the Mississippian-Pennsylvanian boundary in that no continuous phylogeny has yet been established for *Gnathodus*. *Gnathodus* has not been listed among the described faunas from the oldest Pennsylvanian rocks so far studied. Some gnathodids may be present but misidentified which would connect the Mississippian species assigned to *Gnathodus* with those in the Pennsylvanian. A group of specimens which is quite likely to be the ancestor of the oldest recognized Pennsylvanian gnathodids was described by Ellison and Graves (1941, p. 4, 5) as *Cavusgnathus nodulifera*. This was placed in a new genus, *Declinognathodus*, by Dunn (1966), and later was almost simultaneously placed in *Idiognathoides* (Lane, 1967) and *Gnathodus* (Koike, 1967). Although Koike's treatment of these forms appears to be the most reasonable, they may prove to be unrelated to the Mississippian gnathodids, requiring a new genus for them because they would be homeomorphs.

The oldest gnathodids included in the present study for which a substantial, well-documented lineage can be established are from the Lower Mercer Member (Pottsville) and belong to *Gnathodus bassleri* (Harris and Hollingsworth), a species whose status has recently been clarified by Lane (1967). It is not only practical for this study, but important to extend the range of *Gnathodus* into the older Pottsville rocks. First, it is possible to get a more complete picture of the evolutionary changes within the genus, and second, it establishes a firmer foundation from known species, following the phylogeny through previously unknown intermediate stages to later known species.

Gnathodus bassleri departs from many generic definitions of *Gnathodus* in that its carina does not extend to the posterior limit of the platform. Instead, it has two continuous rows of nodes flanking the carina which meet posteriorly behind the carina. The result is a platform that looks very much like *Streptognathodus* and could be considered a homeomorph of it. Most specimens of *Gnathodus* from the Lower Mercer Member belong to this species.

In the Upper Mercer the dominant form carries two rows of nodes, but both fuse to the posterior terminus of the carina rather than extending farther posteriorly to meet behind it. This is designated herein as *Gnathodus* n.sp. A.

Putnam Hill samples are characterized by gnathodids in which the outer row of nodes has become fused to the carina posterior to midlength, but anterior to the terminus. The inner row continues to the terminus of the carina where they fuse as in *Gnathodus* n.sp. A. This second form is designated *Gnathodus* n.sp. B.

The same trend of shortening the outer row of nodes continues through *Gnathodus* n.sp. C, dominant in the Vanport Member. The fusion in this form has migrated to, or is in front of, the outer midpoint of the platform.

A few specimens intermediate between *Gnathodus* n.sp. C and *G. roundyi* have been found both in the Vanport and younger units and are very well represented in some faunas from the Midcontinent region. These intermediate forms lack the outer continuous row of nodes; they have instead a few scattered nodes marking its former location. Generally speaking, the greatest morphological jump is found between samples from the Vanport and Columbiana Members. Stated differently,

less faunal overlap among the gnathodids is present between these two units than any other adjacent pair in the upper Pottsville or Allegheny.

Gnathodus roundyi Gunnell is the dominant form in the Columbiana Member, although *G. dilatus* Stauffer and Plummer also occurs. In *G. roundyi* the outer nodose row has been reduced to a single node located about one-third of the way behind the anterior end of the platform. In *G. dilatus* even this node has disappeared, and the platform bears only a carina and the inner nodose row. Some specimens show the beginnings of a deterioration of the inner row as well. Morphologically, *G. dilatus* is somewhat similar to *Cavusgnathus*.

Gnathodus is rare in the Washingtonville, so rare in fact that it can no longer be used for zonation. The only species represented at all adequately is *G. dilatus*, and consequently one could speak of a "*Gnathodus dilatus* Zone". Finding enough specimens from this unit to identify the zone, however, would be an arduous task. Some specimens from this unit exhibit deterioration of the inner row of nodes, the gaps between the nodes increasing in size, especially near the posterior part of the platform.

A final theoretical form may exist in which the inner nodes have entirely disappeared as well, and only the carina remains, producing a *Spathognathodus* homeomorph. Direct evidence for this is insufficient, but a pair of specimens, both from the Washingtonville, conform fairly closely to this concept (plate 2).

If such a form does exist, it likely marks the end of the genus. *Gnathodus* does not occur in Conemaugh or Missourian rocks

and its extinction seems absolute. Any younger forms with this morphology must be regarded as homeomorphs (Bender and Stoppel, 1965).

This set of evolutionary symmetry-morphology transitions in the series *Gnathodus bassleri* → *G. n.sp. A* → *G. n.sp. B* → *G. n.sp. C* is almost identical to the one for the morphologically similar *Gnathodus girtyi* and its several subspecies in the Mississippian, summarized by Globensky (1967). Lane (1967) has outlined still another example involving the immediate ancestor of *Gnathodus bassleri* (*sensu stricto*) (his *G. bassleri bassleri*) as a subspecies (*G. bassleri symmetricus*) that is nearly, if not completely indistinguishable from my *Gnathodus n.sp. A*. Direct reversals in morphology such as these which produce homeomorphs separated in time by a single intervening species, are not uncommon in platform conodonts (see phylogeny of *Idiognathodus-Streptognathodus*) and necessitates caution in making stratigraphic determinations with these kinds of phylogenetic fluctuations.

The abundance of *Gnathodus* in the upper Pottsville has not been accurately estimated, and no statistical tests have been made on these data. Nevertheless, most samples from the Lower Mercer have ratios *Gnathodus* : *Idiognathodus* (+ *Streptognathodus*, where present) averaging quite close to 1:5. Fewer data are available from the Upper Mercer, but it is obvious that *Gnathodus* is less abundant, and an estimate for the same ratio of 1:10 seems reasonable. This reduction continues into the Allegheny and the Putnam Hill ratio is 1:15. The Vanport in both north and south contains a major resurgence and the ratios average about 1:4. After this temporary return, the abundance of the genus falls off rapidly

in the succeeding units, paralleling the morphologic deterioration. In the Columbiana the ratio is 1:40 and in the Washingtonville, 1:200. The prolific Columbiana samples usually provide enough specimens to be usable, but the 1:200 ratio in the generally much smaller Washingtonville samples makes its use for zonation there unrealistic. Nevertheless, its rarity may itself be of some help, for example, at Washingtonville locality 2, among 41 platforms, there was one specimen of *Gnathodus dilatus*. Although this ratio conforms exactly to that for the Columbiana, 1:40, the scarcity and the fact that it was a specimen of *G. dilatus*, not *G. roundyi*, strongly suggest a Washingtonville assignment. Evidence from the *Idiognathodus-Streptognathodus* ratio also favors the Washingtonville determination here.

The broad-scale picture in these faunas is one in which *Gnathodus* evolves (or perhaps better "devolves") into simpler and simpler forms, concurrently decreasing in abundance, until it becomes extinct. Evidence for this progressive loss of ornamentation and morphologic simplification is more than ample.

And:

"All right", said the Cat; and this time
it vanished quite slowly, beginning with
the end of the tail....
....and ending with the grin,
which remained some time
after the rest of it had gone."

(Dodgson, loc. cit.)

Idiognathodus-Streptognathodus.—These genera cannot logically be separated for this discussion. Indeed, they illustrate another common trend in platform conodont evolution in the redevelopment

of lost morphologic features. Alternation between these two morphologic forms takes place on a broad scale within populations of differing ages through most of the Pennsylvanian. Certain aspects of these phylogenetic changes are also reflected in the growth stages of individuals in any given sample and are ontogenetic as well.

The ancestry of this group is presently unknown. It has been postulated to have come from either *Cavusgnathus* or *Gnathodus*, but no credible phylogeny has been established for either. The earliest Pennsylvanian rocks studied (Lane, 1967, *et al.*) contain neither *Idiognathodus* nor *Streptognathodus*. I have some undescribed Namurian material from England which is also "pre-*Streptognathodus*". The next younger group of described faunas (Harris and Hollingsworth, 1933; Harlton, 1933; Ellison and Graves, 1941; Clarke, 1960; Dunn, 1966; Lane, 1967) contain fully developed *Idiognathodus*. Some samples from the "lower" Pottsville rocks of Kentucky and West Virginia are dominated by streptognathodids transitional to *Idiognathodus* and suggest ancestor-descendant relationships. Units somewhat higher enter into the normal Lower and Middle Pennsylvanian realm in being dominated by *Idiognathodus*, a situation that obtains through the remainder of the Pottsville and Allegheny rocks. Highest Allegheny and lower Conemaugh rocks contain the transition from *Idiognathodus* to *Streptognathodus*. The remainder of the Conemaugh is dominated by *Streptognathodus*, *Idiognathodus* dropping out completely before the highest units are reached. The same, or at least a very similar arrangement is present in the Midcontinent region with *Idiognathodus* perhaps lasting a little longer, but

disappearing completely in the upper Missourian. It reappears well up in the Virgilian Series, presumably "rederived" once again from *Streptognathodus* which had continued after the Missourian "extinction" of *Idiognathodus*. This last impulse of *Idiognathodus* was possibly what prompted Ellison's statement (1941, p. 127) that *Idiognathodus* was derived from *Streptognathodus*: a true statement, but one depending on the part of the column under consideration. This generic seesaw is not as biologically important as generic recognition would make it appear; the "genera" are simply two morphologic expressions within a single biologic group, and their retention as separate entities is only justified by convenience, convention, and biostratigraphic significance. The virtual homeomorphs produced by these fluctuations should not prove too difficult to separate. Representatives of both genera presently have potential biostratigraphic usefulness, which will undoubtedly be both realized and expanded when they are properly studied in sufficient detail.

Idiognathodus is by far the most abundant single genus in the Allegheny collections, amounting to over 20,000 specimens (20,627) or nearly one-half of the total fauna. The occurrences of specimens with the morphology of *Streptognathodus* can be divided into two classes, those which are demonstrably immature forms of *Idiognathodus*, and those which are adult forms properly assigned to *Streptognathodus* and which have evolved from *Idiognathodus*. Although these can be divided, such division is not always easy, nor is it always necessary. The former type is common in all Allegheny units and together the two kinds demonstrate the phylogenies of both genera. In the higher units, especially in the Washingtonville, there is a marked increase in

adult forms that, during ontogeny, retained the longitudinal trough of *Streptognathodus* instead of developing the transverse ridges of *Idiognathodus*. They are the evolutionary pioneers of the shift to *Streptognathodus* in younger rocks. Two species are recognized, *S. cancellosus* and *S. oppletus*, both of which continue into the Conemaugh and both of which are transitional between the two genera. Their separation is rather arbitrary, but has merit both phylogenetically and biostratigraphically.

Ornamentation in *Idiognathodus* is extremely variable and complex. No two specimens are identical, even in a broad interpretation of the word. This complexity makes the group difficult to study. An indirect side effect of this complexity is that it has prompted a tremendous proliferation of specific names, producing a difficult nomenclature. Ellison attempted to bring some order out of this chaos by reducing some 65 specific names to 9 through synonymies. The same treatment was given to *Streptognathodus*. For the latter it has worked well. His philosophy was conservative and the results are reproducible. His similar system for *Idiognathodus*, however, cannot advantageously be used for the present material. To do so would obscure relationships that are present, and would result in illogical groupings, many with little internal relationship. His morphologic approach simply fails phylogenetically because the wrong criteria were selected. As a result I have placed all the idiognathodids from the Allegheny into two species. Both *I. claviformis* (type species) and *I. delicatus* date from the inception of the genus (Gunnell, 1931). A few specimens are assigned with severe reservations to *I. claviformis*. Although the type species of the genus, it appears

to be a rare and incidental side issue of the main morphologic development and is probably polyphyletic as well. All the remainder can be placed into *I. delicatus*, although continuing to follow Ellison's precedent would place them in several additional specific categories, most of which would be phylogenetically, and hence ultimately biostratigraphically, meaningless. The group herein called *Idiognathodus delicatus* therefore contains nearly all of the 20,000-odd idiognathodids from the Allegheny. These forms offer a wealth of morphologic detail which did not remain constant through time. Rather than too few changes, as assignment to a single species might indicate, there are really too many and they are too complex. The only hope for resolving the complex morphologic muddle is by undertaking a comprehensive and detailed biometric analysis of all specimens obtained from the entire range of the genus and from the widest possible geographic area. Such a study could, and probably should, include several hundred of thousands of individual specimens. After, and only after, resolving the morphologic problems, the work can proceed with the taxonomy. Since Ellison attempted to reduce the confusion in his 1941 revision, synonymizing all but 9 of 65 names, the number of names has increased again until, counting the 65 pre-1941 ones which remain forever in competition, we have perhaps 90 to 100 available at present. Some of them will remain valid, of course, and new valid ones will be added by the biometric study just outlined, but such a study is vastly beyond the scope of this work. The differences mentioned can be readily seen in some of the material, others are more difficult to perceive. A tentative step toward defining these differences is arranging the figures of *Idiognathodus*

delicatus on plates 5-8 into ten morphotypes, designated by the Greek letters α through κ . These will be described briefly in the systematics section. The criteria used to separate them may not prove to be at all better than those of any of the previous workers, yet they seem to be the most logical groupings to date. The eighty-one photographs for plates 5 through 8 were sorted into ten piles, each representing a morphotype, several times until the number of morphotypes remained constant and individual figures did not commonly move despite repeated sorting. Morphotypes such as these seem to represent a fairly good cross-section of the population, although the sample is far too small for conclusive results. Sound statistics may completely revise these groupings, but the similarities seem to be moderately strong.

BIOSTRATIGRAPHIC ZONATION

Taxa which are not ubiquitous in the rocks they are supposed to zone are less than ideal for biostratigraphic work. The forms which distinguish the *Cavusgnathus*-biofacies and the two provincial faunas are restricted, and also range throughout the Allegheny with essentially no morphologic change. The burden therefore falls on the truly ubiquitous taxa to provide the necessary criteria for distinguishing biostratigraphic zones. The ubiquitous forms include the following genera, *Gnathodus*, *Idiognathodus*, *Streptognathodus*, *Ozarkodina*, and *Spathognathodus*. The category of "others" also belongs with this group, but is unusable. The final two genera, *Ozarkodina* and *Spathognathodus*, exhibit little if any change and their presence and abundance may be related too closely to

preservation.

The three remaining platform genera do show the necessary changes in both morphology and abundance. *Gnathodus* is, as far as the Allegheny rocks are concerned, a generic entity, distinct from the *Idiognathodus-Streptognathodus* group.

Four methods of zoning Allegheny rocks are possible with these three genera. Two are related to the distribution of genera and the other two with phylogenies within genera.

The genus *Gnathodus* generally decreases in abundance upward through the Allegheny. Decreasing from a high in the Lower Mercer Member (Pottsville), it shows one strong increase in the Vanport contrary to the general decreasing trend. The characteristic ratios have already been listed for the various units, and these can be of great help in identifying them. The Putnam Hill has about one-third as many specimens in relative numbers as the Vanport, the Columbiana has about one-third as many as the Putnam Hill, and the Washingtonville has about one-fifth as many as the Columbiana. Therefore, *Gnathodus* is 50 times more abundant in the Vanport than in the Washingtonville.

Idiognathodus should steadily decrease upward through succeeding units as it is replaced by *Streptognathodus*, its heir. This holds true for all subdivisions except the northeastern Vanport where *Streptognathodus* is grossly under-represented. Ratios between *Streptognathodus* and *Idiognathodus* average 1:30 in the Putnam Hill, 1:10 in the southern Vanport, 1:8 in the Columbiana, and 1:2 in the Washingtonville. The 1:200 ratio of the northeastern Vanport is greatly out of line with any of these. Thus, distribution of genera

coincides with the general trends in 8 out of the possible 10 tests for units/regions. The northwestern Vanport has not been included in these ratios because of the small size of the collections from it, but it appears to fit well with the predictions.

Distributions of taxa at the specific level are inherently more reliable than those of long-ranging genera. The species dealt with form a related group of closely-knit individuals in contrast with comparisons between unrelated genera.

Two methods for utilizing species are immediately obvious from my collections. The one using the phylogeny of *Idiognathodus* may be ultimately the most promising, but cannot presently be used. Some of the morphotypes appear to have considerable promise for this purpose, but the present data are insufficient. The well displayed phylogeny of *Gnathodus* is, on the other hand, easy to use and permits a zonation which can be applied with considerable confidence. The Lower Mercer, Upper Mercer, Putnam Hill, Vanport, and Columbiana can easily be distinguished from each other by a characteristic, most abundant species of *Gnathodus* (fig. 10). The Washingtonville contains too few gnathodids to employ for zonation and its recognition must depend on the great increase in streptognathodids.

Zones.—The zonation developed for the Allegheny is:

1. *Idiognathodus delicatus* s.l. - Streptognathodus cancellosus Zone - Washingtonville Member.
2. *Gnathodus roundyi* Zone - Columbiana Member.
3. *Gnathodus* n.sp. C Zone - Vanport Member(s).

4. *Gnathodus n.sp. B Zone* - Putnam Hill Member.

and for the upper Pottsville:

5. *Gnathodus n.sp. A Zone* - Upper Mercer Member.

6. *Gnathodus bassleri Zone* - Lower Mercer Member.

Age of the two Vanports.-In the discussion of the Vanport stratigraphy (q.v.) the comment was made that the conodont evidence suggests that the southern Vanport is older than the northern Vanport. Differences between the gnathodids are the primary evidence for this conclusion. More specimens from the southern Vanport are assignable to the more primitive species present in the Putnam Hill, *Gnathodus n.sp. B*. Furthermore, the outer nodose row in the ones assigned to the characteristic Vanport species, *G. n.sp. C*, is consistently longer in specimens from the southern Vanport. These differences, small as they are, lead me to believe that the southern Vanport is the older of the two.

INTERREGIONAL CORRELATIONS

In the past, attempts have been made to correlate the several Allegheny marine units with various marine beds in the Illinois Basin and Kansas and Missouri. Some correlation charts actually suggest lateral continuity of these units for distances of up to 1,200 miles. Such estimates of lateral continuity tax credulity, but no one can seriously question that sediments were accumulating more or less simultaneously over much of eastern and midwestern North America during Middle and Late Pennsylvanian time. It has not been proved, and perhaps never can be, that marine sedimentation was truly synchronous over any great distance. If

Figure 10. Conodont zonation of the Allegheny Group and parts of adjacent units.

The Appalachian Pennsylvanian Conodont Zones

Gp	Member	Zonal taxa
CONEMAUGH		
	Lower Brush Creek	<i>S. cancellosus</i> - <i>S. oppletus</i>
ALLEGHENY	Dorr Run Member	Unzoned
	Washingtonville Member	<i>I. delicatus</i> - <i>S. cancellosus</i>
	Columbiana Member	<i>Gnathodus roundyi</i>
	Vanport Member	<i>Gnathodus n. sp. C</i>
POTTSVILLE		
	Upper Mercer Member	<i>Gnathodus n. sp. A</i>
	Lower Mercer Member	<i>Gnathodus bassleri</i>

subsidence were triggered in these other areas in the same manner as has been postulated for the Appalachians, it is unlikely that any individual transgression could be recognized in more than a single basin. Nevertheless, some marine unit in Kansas or Missouri or Illinois must be nearest in age to each marine bed in the Appalachians. However, the larger the area covered by transgressive marine units in the Midcontinent, the greater must be the diachroneity within the unit.

Various sources display different correlations in chart or cross-section form. The Geological Society of America's Pennsylvanian Correlation Chart (1944) offers the following approximate correlations:

<i>Midcontinent</i>	<i>Illinois Basin</i>	<i>Eastern Ohio</i>
Worland	Piasa	
Myrick Station	Bereton	Washingtonville
Ardmore	Oak Grove	Columbiana
Tiawah	Seahorne	Vanport
Seville	Curlew	Putnam Hill

Moore, who edited the Geological Society of America's chart presented another revised one fifteen years later (1959, p. 42, 43):

<i>Midcontinent</i>	<i>Illinois Basin</i>	<i>Eastern Ohio</i>
		Dorr Run
		Washingtonville
Ardmore	Oak Grove	Columbiana
?	Seahorne	Vanport
		Putnam Hill

One of the differences between these charts can be explained

by the Putnam Hill being shown to pinch out to the west on the later chart and the Curlew Limestone of Illinois to continue eastward across the Cincinnati Arch to form a continuous sheet with the Zaleski Flint in Ohio. Not only is the Zaleski Flint a facies of extremely limited areal extent, but it can be shown to be a facies of the Putnam Hill Member.

Material from the Myrick Station Member contains numerous gnathodids, far more than from the Washingtonville, and they represent more primitive species than *Gnathodus dilatus*. Accordingly, I believe that the Washingtonville is younger than the Myrick Station. The gnathodids from the Ardmore Member are slightly more primitive than those from the Columbiana, suggesting that, it too, is probably younger than its supposed equivalent. Therefore, the Columbiana would be younger than the Ardmore and older than the Myrick Station. Like the Conemaugh conodont correlations with the Midcontinent (Merrill, 1964, p. 50-54), those for the Allegheny suggest that the Appalachian units are generally younger than they have traditionally been regarded.

NON - PLATFORM CONODONTS

For completeness, some discussion of the non-platform taxa is necessary. The platforms already have been discussed in detail and will receive still more attention in the systematics. The non-platform taxa were heretofore merely listed with their groups of associates and illustrated in figures 3-6.

BLADES

Ozarkodina spp.-Several species of this genus are present in the Allegheny collections, including the well established *O. delicatula* (Stauffer and Plummer, 1932). The genus is especially difficult to study because of fragmentation; nearly complete individuals are necessary for specific determinations, although fragments are easily assigned generically. It is likely that *O. delicatula* is not the only species occurring in the Midcontinent region either, and consequently no special significance is attached to the occurrence of the genus or any of its species. There is some indication that there may be a species restricted to the *Cavusgnathus*-biofacies, but this cannot be stated with certainty with available material.

Spathognathodus spp.-Ellison's *Spathognathodus minutus*, a robust spathognathodid, is present and the dominant species. The tiny *S. coloradoensis* Murray and Chronic (1965) seems to be an Appalachian form. Its relationships are not clear, but it does not appear to be a growth stage of some other species such as *S. minutus* as its small size might indicate. Presently the genus, like *Ozarkodina*, has no special significance attached to its distribution, although, based on Ellison's statement (1941, p. 120), it would

appear that the genus is far more common in the Appalachians than in the Midcontinent.

BARS

Hibbardella subacoda.—This species is a characteristic fossil in the Midcontinent provincial faunas.

Hibbardella n.sp. 1 and 3.—Although both of these occur in the Allegheny Group, *H.* n.sp. 1 is far more common in, and characteristic of, some of the faunas from the Conemaugh Group. *Hibbardella* n.sp. 1 is a massive form with a very heavy posterior process; widely spaced, strongly recurved, moderately large denticles and cusp; relatively small, recurved lateral processes with small denticles; and a deep, long basal cavity. Nothing similar to it has been described from the Pennsylvanian. *Hibbardella* n.sp. 3, more common in the Allegheny, is less massive, more blade-like, with an erect cusp, closely spaced denticles and the lateral processes fused to the anterior edge of the cusp, giving the unit a "T" outline in oral view. It is not strongly similar to other Pennsylvanian hibbardellids. Both these species, because of their concentrations in conjunction with *Cavusgnathus*, are considered to be members of the nearshore biofacies.

Hibbardella n.sp. 2.—Murray and Chronic (1965, pl. 73, figs. 3-5) illustrated their *Hibbardella acuta*, which is quite similar to this species and may in fact prove to be a senior synonym of it. A small, fragile form that is too often not preserved, this species occurs with the Appalachian provincial fauna.

Hindeodus spp.—At least three and probably four or five

species of this genus occur in the Allegheny rocks. All of them are new, unless the form described by Murray and Chronic as *Hibbardella obtusa* (pl. 73, figs. 8, 9) proves to be a senior synonym of one of them. All species exhibit the characteristic symmetry or subsymmetry of the type species, *Hindeodus imperfectus* (Rexroad). Although the genus will probably prove to have Midcontinent representatives, it is presently considered, *in toto*, a part of the Appalachian provincial fauna. Murray and Chronic published on material from the only predominantly Appalachian provincial fauna to appear in the literature.

Ligonodina lexingtonensis (Gunnell) and *L. typa* (Gunnell).-

These two species are quite characteristic of Midcontinent faunas. The former seems to be the more restricted (*i.e.* less commonly a "line-crosser").

Ligonodina n.sp. 4.-This is probably no longer a new species and quite likely should never have been referred to *Ligonodina*. *Hindeodella multidenticulata* and *Hindeodella megadenticulata*, both of Murray and Chronic, are quite likely synonyms both of this form and of each other. It is my opinion that they are less reasonably assigned to the hindeodellids than to the ligonodinids, although not strictly compatible with either genus. They are probably an outgrowth of the *Hindeodus* series of symmetry variations, and it may be necessary eventually to build a new genus around them. This is an abundant Appalachian form.

Ligonodina n.sp. 10.-Generic assignment of this form is also somewhat questionable as it shows strong hindeodellid characteristics as well. Along with *Ligonodina n.sp. 4*, it probably served a more

ligonodinid than a hindeodellid function in the body of the organism which bore it. No forms really closely related to this species have been described. It is very characteristic of the *Cavusgnathus*-biofacies, although rather fragile and consequently is rarely preserved.

Lonchodina spp..-At least four species of this genus are present in the Appalachians. A rare species has been found in the *Cavusgnathus*-biofacies in the marine units of the Conemaugh Group, and presumably may also be present in the Allegheny. A second, also uncommon in occurrence, appears to be part of the Appalachian provincial fauna. These two species are new and not closely similar to the other two described species, *Lonchodina clarki* (Gunnell) and *L. ponderosa* Ellison, which are present, far more abundant, and indicative of the Midcontinent provincial fauna. The preponderance of these last two species is sufficiently great, that for practical purposes, we may consider the entire genus to belong to the Midcontinent faunal province.

Metalonchodina spp..-Although not especially common, this distinctive genus is a good Midcontinent indicator. Most specimens are assignable to *M. bidentata* (Gunnell), although other species may be present.

Neoprioniodus spp., except n.spp. 7 and 10.-In general terms this category consists of the two Midcontinent species *Neoprioniodus conjunctus* (Gunnell), and *N. bulbosus* (Ellison).

Neoprioniodus n.sp. 7.-This is a fragile form, which commonly fragments in much the same manner as *Hibbardella* n.sp. 2, and has no close Pennsylvanian relatives. It is morphologically similar to

the Late Mississippian species *N. camurus* Rexroad and is an Appalachian species.

Neoprioniodus n.sp.10.-Like the preceding, this species has no close relatives in the Pennsylvanian, but is similar to the Mississippian *Neoprioniodus loxus* Rexroad. This is a *Cavusgnathus*-biofacies form in the Allegheny, although another new species replaces it in younger rocks.

New genus A, n.sp. 3.-Fragments and sometimes rather complete specimens of this form have been figured by several authors, starting with Gunnell (1933, pl. 31, fig. 40). Most commonly it has been assigned to *Ozarkodina* or *Ligonodina*, and the best illustrations are to be found in Murray and Chronic (1965, pl. 73, fig. 16 as *Ligonodina* sp.; fig. 18 as *Ozarkodina* sp.; and fig. 29 as *Ozarkodina cf. O. curvata* Rexroad). This is a ligonodinid-like blade or semi-blade, whose genetic relationship to *Ozarkodina* is obvious. Some specimens tend to become much more bar-like than blade-like and because of them the form is presently considered among the bars rather than the blades. This new genus should include *Ozarkodina curvata*. It is one of the most characteristic Appalachian forms.

New genus B, n.sp. 1.-The history of this form closely parallels that of the new genus above. It has most commonly been described as "*Synprioniodina* sp." (Murray and Chronic, 1965, pl. 73, figs. 10, 11). Actually it is an abundant and important representative of the symmetry variation series derived from *Hindeodus*. It is also a member of the Appalachian provincial fauna.

Others.-Included in this inevitable category are two distinct and fairly common genera, as well as probably several rarer ones,

and all generically indeterminable fragments. As such, it is both large and diverse. Its size, however, is not entirely the result of inability to identify specimens, for commonly this contribution consists almost entirely of fragmentary specimens of the genus *Hindeodella*, as well as specifically determinable specimens of the same genus. There are no fewer than six species (four new) of *Hindeodella*, as well as the usual numerous bar fragments. All species of *Synprioniodina* (at least three, two of which are new) are also placed in this category. Too little is known, taxonomically, stratigraphically, or geographically about these forms to further subdivide and assign them for my purposes. Furthermore, in any given sample, they are too few in number to be significant. The fragments of *Hindeodella* are certainly ubiquitous, as are the indeterminable fragments, and the category as a whole must be so considered, although again, some of the identifiable species are possibly restricted.

CONCLUSIONS

Four categories of conclusions were reached from this study of Allegheny conodonts.

First, the Allegheny platform conodonts can be used to formulate a workable biostratigraphic zonation. The part of the column studied had not been zoned previously with conodonts, and this zonation promises to be especially useful because of the widespread and abundant distribution of the taxa involved, and their apparently greater stratigraphic restriction than that of most Pennsylvanian biota.

Ten biostratigraphic units can now be recognized in the upper Pottsville, Allegheny, and Conemaugh rocks. At least one older zone is known to occur in the Pottsville rocks of Ohio, giving a total of not fewer than 11 zones based on conodonts. Fusulinid research has produced only six zones for the entire Ohio Pennsylvanian column and many of the units involved have produced fusulinids at only a few localities. Despite the confidence commonly placed in fusulinids for Pennsylvanian biostratigraphy, they are certainly far less suitable than conodonts for the same purpose in these rocks of the Appalachian Pennsylvanian. By extension the conodonts should be the more useful when comparisons with other areas are made.

Second, the Allegheny marine units all exhibit changes in the ratios of conodont taxa laterally on a small geographic scale. These changes can only be attributed to environmental control and give rise to a nearshore, *Cavusgnathus*-biofacies, and an offshore, *Idiognathodus*-biofacies. This conclusion is at variance with

commonly held beliefs about the invariability of contemporaneous conodont faunas but is also demonstrated in Pennsylvanian rocks of other areas. The close proximity of the two biofacies, stratigraphically and laterally, along with other evidence, precludes any other interpretation. This conclusion may prove the most valuable contribution of this study.

Third, there are faunal differences on a broad scale which appear to be independent of the biofacies and biostratigraphic differences just mentioned. Two intermingling, but locally unmixed, end-member groups of taxa can be recognized. One group, originally described in the pioneer works of Gunnell, Stauffer and Plummer, and Ellison, is considered characteristic of the Midcontinent region, although it occurs in part of the Appalachian column. The other, consisting mostly of new taxa, is the dominant group in the Appalachians, and is present (albeit mostly undescribed) in the Midcontinent as well. These faunas are presently considered to represent two provincial faunas, named for the regions in which they are more common, or at least better known. Although the present evidence favors a provincial interpretation, better evidence in the future may establish that these two groups represent biofacies also, not directly related to the other pair of biofacies. From the point of view of our long-ranging knowledge of the totality of Pennsylvanian conodont faunas, this second exception to contemporaneous uniformity may eventually prove more significant than the readily demonstrable biofacies. Neither of these departures from uniformity obscures the biostratigraphically useful changes in the faunas brought about by evolution.

Fourth, the contributions of this study to the systematics of Pennsylvanian conodonts have some significance in their own right an addition to their secondary implications for biostratigraphy. *Cavusgnathus* presents nothing new or surprising, but *Gnathodus* shows a consistent, unidirectional set of changes in upper Pottsville and Allegheny rocks. Three new and three previously described species, along with what will probably prove to be two additional new species, trace the phylogeny of *Gnathodus* from species previously known in older Pennsylvanian rocks to the very end of the range of the genus, incorporating other, younger, previously described species as well. This study has filled in some important gaps in the lineage of the genus.

Although no significant progress was made or even attempted in unravelling the morphological and nomenclatural complexities of the *Idiognathodus-Streptognathodus* lineage, the approach of selecting ten morphotypes, α through κ , of *Idiognathodus delicatus* has some promise for future biometric studies.

SYSTEMATIC PALEONTOLOGY

GENUS *CAVUSGNATHUS* HARRIS AND HOLLINGSWORTH, 1933.

Type species: *Cavusgnathus altus* Harris and Hollingsworth, 1933.

Diagnosis.-Elongate platform conodonts having the aboral surface of the platform excavated into an elongate, deep basal cavity; oral surface of platform bears a longitudinal trough lacking a carina, bordered by cross-ridged to finely nodose parapets. Position of blade usually eccentric, commonly continuous with outer parapet posteriorly.

Remarks.-Lane (1967) erected a new genus, *Adetognathus*, which if accepted would embrace all Pennsylvanian conodonts previously referred to *Cavusgnathus*. He employed three criteria for separating these genera. Previous workers had noted that the Mississippian species assigned to *Cavusgnathus* consisted entirely of dextral individuals, and species from Pennsylvanian rocks contained, in separate species, both dextral and sinistral specimens. Lane used the ambidextrous nature of the younger specimens as a part of his discussion of differences. The two genera he recognized are, in addition, supposed to possess minor differences in the denticulation of the free blade. The single distinctive characteristic on which he actually defined *Adetognathus* is a fixed blade shorter than its free blade. In all other respects, the genus, in large part at least, is indistinguishable from *Cavusgnathus* in which the fixed blade is equal to or longer than the free blade.

In overall appearance, *Cavusgnathus unicornis* (Late Mississippian) and *Cavusgnathus* (= *Adetognathus fide* Lane) *gigantus* (entire

Pennsylvanian) are virtual homeomorphs. Indeed, some authors have expressed uncertainty about separating them (Rexroad and Collinson, 1961, p. 5, 6). Outer lateral views of the two species cannot be objectively distinguished. According to Lane's definition, the Mississippian form will possess a well-developed fixed blade and the Pennsylvanian one will not. The Lower Pennsylvanian specimens he assigned to *Adetognathus gigantus* conform to his concept and, at best, have weakly-developed fixed blades. It would not be difficult to duplicate Lane's figures from my Allegheny material. On the other hand, it is quite obvious from my plate 1 (for example, figures 35, 36, 38) that many younger specimens of this species more closely resemble *C. unicornis* in the presence of a strong fixed blade than they do his selected specimens.

While admitting that his criteria have merit, and as generalizations are largely correct, I do not believe that they are sufficient for the establishment of a new genus. What significance should be attached to dextral plus sinistral *vs.* dextral ones alone cannot presently be assessed. If the species in question prove to belong to a single phylogenetic lineage, as Lane suggests, and which is probable, then the addition of sinistral elements near the beginning of the Pennsylvanian is of some importance, although not necessarily worth generic recognition. According to Lane, the younger forms have the higher denticles of the free blade grouped near its anterior end and the opposite is true of older specimens. This is probably true as a generalization, but one with numerous exceptions. The fixed/free blade relationship is at best of doubtful

value.

Cavusgnathus lautus Gunnell was chosen as the type species of *Adetognathodus* by Lane. This species is sinistral, has the denticle arrangement he describes, and little or no fixed blade. These are relatively minor differences from a pattern otherwise identical with several Mississippian cavusgnathids.

For these reasons I reject *Adetognathus*.

When he proposed *Cavusgnathus lautus* and *C. gigantus*, Gunnell evidently assumed that the *-gnathus* stem in *Cavusgnathus* was masculine, although he placed feminine endings on both specific names in places in his text. During the 35 years since his work, names ending in *-gnathus*, which constitute a large proportion of all conodont generic names, have almost universally been treated as feminine because γναθός has been recognized to be a feminine noun in Greek. The International Code of Zoological Nomenclature, Article 30(a)(3), specifically lists several feminine Greek nouns which are to be treated as though they were masculine because of their endings. Among them is γναθός. *Cavusgnathus lauta* and *C. giganta* therefore once again become *C. lautus* and *C. gigantus*, respectively.

Cavusgnathus lautus Gunnell, 1933.

Plate 1, Figures 1-24.

Cavusgnathus lauta Gunnell, 1933, p. 264; Ellison, 1941, p. 126, pl.

21, figs. 47, 48; _____ & Graves, 1941, p.2, pl. 3, fig. 2;

Branson, 1944, p. 325, pl. 45, figs. 47, 48; Cooper, 1947,

p. 269; Sturgeon & Youngquist, 1949, p. 383.

Cavusgnathus lautus Gunnell, 1933, p. 286, pl. 31, figs. 67, 68;

Fay, 1952, p. 77.

non Cavusgnathus lautus Gunnell, 1933, p. 286, pl. 33, fig. 9.

Cavusgnathus missouriensis Gunnell, 1933, p. 286, 287, pl. 33,

fig. 11 only; Lane, 1967, p. 934.

? *Cavusgnathus* cf. *lauta* Fúlfaro, 1965, p. 37.

Cavusgnathus spatha Dunn, 1966, p. 1297, 1299, pl. 157, figs. 3a-c
only.

Adetognathus lauta (Gunnell). Lane, 1967, p. 933, 934, pl. 121, figs.
1-5, 7, 10, 11, 15, 17, 18.

Adetognathus unicornis (Rexroad & Burton). Lane, 1967, p. 930, 931,
pl. 119, figs. 17?, 18?, 19?, 20, 21 only.

pars Adetognathus missouriensis (Gunnell). Lane, 1967, p. 934.

Description.-In lateral view aboral edge of free blade moderately straight, unarched, commonly one-half the length of the platform or more, rarely as long as the platform; platform only slightly arched on outer side, inner side more conspicuously so, parapets overhanging, producing a pronounced crease about one-third of the distance above the aboral margin of both inner and outer sides of the platform.

In oral view platform narrow, moderately bowed, acutely pointed posteriorly, parapets subequal, outer parapet straighter, lower, less flaring laterally, with less pronounced overhang, inner parapet more laterally bowed, higher, flaring laterally and orally to a maximum near mid-length, more overhanging; both parapets ornamented with laterally elongate nodes and remnants of transverse ridges, obsolescent into the trough, transverse ridges normally longer on flaring inner side, forming a radial, fan-like pattern in

some specimens; trough narrow, deep, smooth bottomed, concave inward.

In aboral view platform narrowly and shallowly excavated with slight and gradual deepening in anterior one-third; lateral flange-like aprons present, usually narrow; inner aboral margin not extended aborally as far as outer, paralleling the relationship between the parapets on the oral surface and producing a rhomboid cross-section for the platform.

Remarks.—This species consists entirely of sinistral specimens. It lacks the conspicuous large denticles usually developed in *Cavusgnathus gigantus*, and does not have the rounded posterior termination characteristic of *C. flexus*. The flaring inner parapet and the acute angle it forms as it joins the outer parapet posteriorly are also distinctive features.

Dunn united in his *Cavusgnathus spatha* dextral and sinistral specimens which have one or more node-like denticles developed at the posterior end of the platform. Other species of *Cavusgnathus*, including *C. altus*, the type species, are known which possess this posterior blade-like arrangement. Dunn's specimens are, in all important respects, otherwise indistinguishable from *C. gigantus* and *C. lautus*, respectively. Compare his pl. 157, figs. 3a-c with my pl. 1, figs. 11, 24.

Lane made *Cavusgnathus lautus* the type species of *Adetognathus*, and placed several representatives of that species in the genus. He also assigned several additional specimens to *Streptognathodus unicornis* Rexroad and Burton and assigned these to *Adetognathus* also. The specimens he assigned to *A. unicornis* can

be easily and reasonably assigned to *Cavusgnathus lautus* and *C. gigantus*. He erred in accepting *C. missouriensis* as a valid dextral species. Gunnell based *C. missouriensis* on cotypes, pl. 33, figs. 10 and 11. Figure 10 is a normal representative of *C. gigantus*, and fig. 11 is distinctly a *C. lautus* as pointed out by Ellison (1941) who erred in the other direction by placing the entire hypodigm of the species in synonymy with the left-sided *C. lautus*. Furthermore, there is reason to believe that Lane's rejection of *C. flexus* Ellison is questionable.

Material.—From the Allegheny 1,642 specimens, distributed as follows: Putnam Hill 91, Vanport 1,353, Columbiana 161, Washingtonville 37.

Distribution.—Throughout the Pennsylvanian in the Appalachians, Midcontinent and other areas where Pennsylvanian cavusgnathids have been reported. Apparently ranges into the Permian.

Cavusgnathus gigantus Gunnell, 1933.

Plate 1, Figures 25-48.

Cavusgnathus gigantea Gunnell, 1933, p. 264.

Cavusgnathus gigantus Gunnell, 1933, p. 286, pl. 33, figs. 7, 8;

Fay, 1952, p. 77.

Cavusgnathus missouriensis Gunnell, 1933, p. 286, 287, pl. 33, fig. 10 only.

? *Cavusgnathus lautus* Gunnell, 1933, p. 286, pl. 33, fig. 9.

Cavusgnathus giganta Gunnell. Ellison, 1941, p. 125, pl. 21, figs.

44, 45, 49; _____, & Graves, 1941, p. 2, pl. 3, fig. 3;

Branson, 1944, p. 325, pl. 45, figs. 44, 45, 49; Cooper,

1947, p. 269; McLaughlin, 1952, p. 620, pl. 83, figs. 3, 4, 6, 7.

Cavusgnathus arca Sturgeon & Youngquist, 1949, p. 383, pl. 75, figs. 11, 12.

non Cavusgnathus arca Sturgeon & Youngquist. Bishoff, 1957, p. 19, pl. 2, figs. 10a, b.

Cavusgnathus spatha Dunn, 1966, p. 1297, 1299, pl. 157, figs. 7, 8 only.

Adetognathus giganta (Gunnell). Lane, 1967, p. 931-933, pl. 120, figs. 16, 18, 19, pl. 121, figs. 8, 12, 13, 16.

Adetognathus unicornis (Rexroad & Burton). Lane, 1967, p. 930, 931, pl. 119, fig. 16 only.

Adetognathus sp. Lane, 1967, p. 934, pl. 122, figs. 3, 8.

Description.-In lateral view, aboral edge of free blade may be straight, but commonly arched rather steeply, an effect strengthened by the series of denticles decreasing in height anteriorly; free blade short, commonly less than half the length of the platform, fixed blade of variable length, dominated by a very large denticle at its posterior limit, platform slightly to strongly arched, parapets nearly equal in height with the parapets overhanging slightly with or without well developed creases.

In oral view, platform wide, moderately bowed, prow-shaped posteriorly, characteristically somewhat constricted just to the rear of the fixed blade, flaring laterally posteriorly from the constriction; parapets commonly broad, sinuous, overhanging, of about equal height, ornamented with transverse ridges and laterally elongate nodes obsolescent into the median trough; trough wide, shallow,

slightly sinuous, concave inward, smooth bottomed.

In oral view unit slightly narrower at aboral margin than at oral margin, excavated into a long, narrow basal cavity with steep slopes into a generally shallow center; lateral flange-like aprons present, variable, usually narrow; inner aboral margin commonly higher than outer one, as in *C. lautus*, but unlike that species, this is not reflected in the height of the inner parapet; because of this the cross-section of the platform is more nearly a trapezoid than a rhomboid.

Remarks.—This species is usually separated from other Pennsylvanian forms by the possession of a very large denticle at the junction of the blade and the outer parapet. *Cavusgnathus gigantus* is an exclusively "right-handed" species. The large denticle is not invariable. Some specimens have several smaller, high denticles at the same location in lieu of one especially large one (pl. 1, figs. 30, 38, 43).

Perhaps more distinctive than the large denticle are the parapets, which are about the same height, commonly sinuous, and meet posteriorly in a broad vee.

Specimens that Dunn named *Cavusgnathus spathus* include forms assignable to this species, although the holotype belongs to *C. lautus*. Compare pl. 1, fig. 43 with Dunn's pl. 157, figs. 7, 8.

Lane also assigned *C. gigantus* to *Adetognathus*. Part of *A. unicornis*, as he treated it, is closer to *C. gigantus* than to the original *Streptognathodus unicornis* of Rexroad and Burton. His *Adetognathus* sp. is an even more characteristic development of *Cavusgnathus gigantus* (compare his pl. 122, figs. 3, 8 with my pl. 1,

figs. 35, 39, 41, 42, 47, etc.).

Material.--From the Allegheny 1,516 specimens, distributed as follows: Putnam Hill 81, Vanport 1,255, Columbiana 145, Washingtonville 35.

Distribution.--Like that for *C. lautus*.

GENUS *GNATHODUS* PANDER, 1856.

Type species: *Gnathodus mosquensis* Pander, 1856.

Diagnosis.--Platform conodonts in which the entire aboral surface is excavated into a wide and deep basal cavity. The oral surface bears a longitudinal, usually median, carina, continuing posteriorly from the blade, to or nearly to the posterior end of the platform. Ornamentation lateral to the carina may consist of nodes, parallel, transverse, or radial ridges, or combinations of these on either side, normally more ornamented on the inner side of the carina.

Remarks.--As presently interpreted, this is a highly variable taxon. Continuous phylogeny of the genus across the Mississippian-Pennsylvanian boundary is in question, making the assignment of Pennsylvanian species to the genus somewhat provisional. Koike (1967) has, correctly in my opinion, assigned forms to *Gnathodus* which had been placed elsewhere by other authors. His recognition that *Cavusgnathus nodulifera* as described by Ellison and Graves probably belongs here is a step in the proper direction and may help to establish the connection between the groups of species assigned to *Gnathodus* in the two systems. The upper Pottsville and Allegheny forms constitute a single lineage not directly affected by these uncertainties.

Gnathodus bassleri (Harris and Hollingsworth, 1933).

Plate 2, Figures 16-19.

Polygnathus bassleri Harris & Hollingsworth, 1933, p. 198, 199, pl.

1, figs. 13a-e; Fay, 1952, p. 150.

Polygnathus wapanuckensis Harlton, 1933, p. 15, pl. 4, figs. 13a-c;

Fay, 1952, p. 161.

Streptognathodus wapanuckensis (Harlton). Branson & Mehl, 1937, p.

177; Elias, 1956, p. 120, pl. 3, figs. 67-69.

Streptognathodus bassleri (Harris & Hollingsworth). Branson & Mehl,

1937, p. 178.

Gnathodus wapanuckensis (Harlton). Ellison & Graves, 1941, p. 2, pl.

2, figs. 15, 17, *only*; Fay, 1952, p. 97.

? *Gnathodus websteri* Youngquist & Downs, 1949, p. 163-165, pl. 31,

figs. 4, 5; Fay, 1952, p. 97.

non Gnathodus wapanuckensis (Harlton). Koike, 1967, p. 300, pl. 1,

figs. 22-25.

Gnathodus bassleri bassleri (Harris & Hollingsworth). Lane, 1967,

p. 934, 935, pl. 120, figs. 1, 3-5, 9-12, 15, pl. 123, figs.

2-4, *non* figs. 1, 5.

Gnathodus bassleri symmetricus Lane, p. 935, 936, pl. 120, figs.

13, 14 *only*.

Description.-In oral view, blade relatively straight, platform lanceolate, greatest width in anterior one-third, pointed to acutely rounded posteriorly; blade continued posteriorly on platform as a fairly straight carina composed of a series of rounded to slightly compressed nodes, less evenly spaced posteriorly; outer parapet

essentially parallel to carina, bearing discrete, transversely elongate, wedge-shaped nodes in a semi-radial pattern and dying out into the depressed area bordering the carina; inner row of nodes like outer row, joining the outer row behind the carina; carina separated from parapets by a deep trough.

In lateral view parapet outline as high or higher than the carina; platform as high as wide with vertical to slightly overhanging sides and rear; blade high, highest denticles located in anterior one-third.

In aboral view, basal cavity wide and deep, widest in anterior one-third and deepest near widest point, bordered by thin shelf-like flanges, basal cavity continues anteriorly as a groove along the aboral edge of the blade.

Remarks.—The nomenclatural history of the species is as interesting as it was confused. Harlton's name was generally accepted until the priority and identity of Harris and Hollingsworth's named was outlined by Lane.

Lane (1967, p. 935) stressed the asymmetry of the platform in this species. My specimens show trends toward the strong asymmetry found in younger species of the genus, but they are more remarkable for their symmetry than for their departures from it.

Homeomorphy between this species and *Streptognathodus* is strong, and the assignment by Branson and Mehl, later followed by Elias, was not entirely unreasonable.

Koike's specimens have carinae extending to the posterior of the platform and are not logical representatives of this species. *Gnathodus websteri* of Youngquist and Downs presents special problems.

The holotype, which I have reillustrated (pl. 2, fig. 20), is the only known specimen. Its age cannot be established, its preservation is poor, the trough is partially filled with matrix, the original figures are misleading, and the posterior tip of the platform is missing. The carina and nodose rows are more subdued than usual for gnathodids and some abrasion may have modified them. It may be conspecific with *Gnathodus bassleri*, or *G. n.sp. A*, or perhaps even *G. n.sp. B*, if the outer row of nodes really ends short of the posterior terminus as it appears to do. Assignment of this single specimen to any species is not possible at present.

Material.-Most of the 303 gnathodids currently available from the Lower Mercer Member, a few additional specimens from the Upper Mercer Member, and 1 specimen from the Putnam Hill Member.

Distribution.-In the Appalachians as shown above, Marble Falls Limestone of Texas, Dimple Limestone of Texas, Wapanucka and other Morrowan and Atokan units of Arkansas and Oklahoma.

Gnathodus n.sp. A.

Plate 2, Figures 8-15.

Gnathodus wapanuckensis (Harlton). Ellison & Graves, 1941, p. 2, pl. 2, figs. 13?, 14, 16 only.

Gnathodus sp. Ellison & Graves, 1941, p.2, pl.2, fig. 11.

Gnathodus roundyi Gunnell. Murray & Chronic, 1965, p. 598, pl. 71, figs. 3, 4 only.

cf. *Gnathodus bassleri symmetricus* Lane, 1967, p. 935, 936, pl. 120, figs. 2, 17 only, pl. 121, figs. 6, 9.

Description.-In oral view, unit slightly bowed, blade

relatively straight, platform lanceolate, greatest width in anterior one-third, pointed to acutely rounded posteriorly; blade continued posteriorly on platform as a fairly straight carina composed of a series of rounded to slightly compressed nodes, less evenly spaced posteriorly; outer row of nodes parapet-like, essentially parallel to carina, consisting of discrete, transversely elongate nodes which decrease in width toward the carina, producing wedge-shaped nodes, dying out into the depressed area bordering the carina; inner row of nodes most commonly like outer row, in some specimens the wedge-like shape of the nodes causes the inner row to become more like transverse ridges than nodes, resulting in a radial, fan-like pattern; both rows of nodes converge sharply or gradually to meet the posterior terminus of the carina, fuse with it, and produce a single node which forms a part of all three rows; trough-like area bordering carina generally deep.

In lateral view, the continuous nodose rows produce a high parapet outline, as high or higher than the carina, the platform commonly being as high as wide with vertical to slightly overhanging sides and rear; blade high and strong, highest denticles located in anterior one-third.

In aboral view the basal cavity wide, widest in anterior one-third, deep, deepest near widest point, bordered by thin, shelf-like flanges, basal cavity continues anteriorly as a groove on the aboral edge of the blade.

Remarks.-This species differs from *G. bassleri* (or *G. b. bassleri*) in having both parapets fused to the posterior terminus of the carina. Presently I have no grounds, either morphologic or

phylogenetic to separate this species from *G. b. symmetricus* of Lane. His subspecies should be older and the ancestor of *G. b. bassleri*. I believe that they are homeomorphs. Perhaps my species shows more tendency for the inner nodose row to be more ridge-like and for the platform to be generally wider, but these are not compelling enough evidence to positively separate them. Several of Ellison and Graves' specimens and one of Murray and Chronic's seem to fit this morphologic definition well. Whether they belong to the ancestor or the descendant of *G. bassleri sensu stricto* is uncertain, but the other gnathodids of Murray and Chronic suggest that their material is younger than *Gnathodus bassleri s.s.*

Material.—Some few of the 303 specimens in the Lower Mercer collections, the majority of the 161 specimens in the Upper Mercer Member, 6 specimens from the Putnam Hill Member, and 5 from the Vanport Member.

Distribution.—The only certain distribution for this taxon is outlined above for the Appalachians, but it is probably represented in the Minturn Formation of Colorado and possibly from the Dimple Limestone of Texas.

Gnathodus n.sp. B.

Plate 2, Figures 2-7, Plate 3, Figure 19.

Gnathodus roundyi Gunnell. Murray & Chronic, 1965, p. 598, pl. 71, figs. 1, 2 only.

Gnathodus cf. roundyi Gunnell. Koike, 1967, p. 299, 300, pl. 1, figs. 27, 28.

Description.—In oral view, unit gently bowed, platform roughly

lanceolate, greatest width in anterior one-third, pointed to broadly rounded posteriorly, blade relatively straight, continued as a straight to slightly sinuous carina to the posterior terminus of the platform, discrete for one-half to two-thirds of its length; outer parapet either parallel to or flaring away from the carina in the anterior portion, closing toward the carina in the posterior half of the platform so that the nodes of this row fuse with those of the carina to produce a single row of transversely elongate nodes in the posterior half of the platform; inner row of nodes transversely elongate, in some specimens almost becoming transverse ridges, ornamenting a parapet which extends to the posterior end of the platform where it fuses with the terminal node of the carina; trough-like groove on inner side of carina extending almost the entire length of the platform, corresponding groove on outer side shallows and terminates posteriorly as the parapet and carina merge.

In lateral view the parapets, whether discrete from or fused with the carina, are high, almost as high as the carina; platform as high or nearly as high as wide, with vertical to slightly overhanging sides and rear; blade high, highest denticle in anterior one-third.

In aboral view, the basal cavity is wide and deep, decidedly asymmetric, more expanded on inner side throughout full length of platform, more expanded anteriorly, more restricted posteriorly on outer side, bordered by shelf-like flanges, basal cavity continued anteriorly as a groove on the aboral edge of the blade.

Remarks.-The degree of fusion of the outer row of nodes and the carina is somewhat variable. In many specimens it is as full and complete as the above description would indicate and the two

rows meet to form a single elongate node. In other specimens, some trace of longitudinal separation remains between the pair. These latter, with the two rows closely spaced and parallel, but with a noticeable sulcus separating them, are considered to have attained fusion for purposes of defining this species.

Murray and Chronic's specimen belongs here with little doubt. Koike's figures are difficult to interpret, but the outer row of nodes disappears in the posterior half of the platform, presumably by fusion with the carina.

Material.—Some specimens from the Pottsville, especially the Upper Mercer Member, 116 specimens from the Putnam Hill Member, and 85 from the Vanport Member.

Distribution.—As above for the Appalachians, the Minturn Formation of Colorado, and probably the Kodani Formation of Japan (Honshu).

Gnathodus n.sp. C.

Plate 2, Figure 1, Plate 3, Figures 20-26.

Gnathodus roundyi Gunnell. Murray & Chronic, 1965, p. 598, pl. 71, figs. 5, 6 only.

Description.—In oral view unit gently bowed, platform roughly lanceolate, greatest width in anterior one-third, pointed posteriorly, blade relatively straight, continued as a sinuous carina to the posterior terminus of the platform; outer nodose row commonly consists of a few (up to 4 or 5) large discrete nodes anteriorly, followed by several smaller ones posteriorly which fuse with the nodes of the carina for over one-half the length of the platform, producing

posteriorly a single row of transversely elongate, commonly undivided nodes; inner parapet commonly bearing laterally elongate nodes, many of them nearly ridges, arranged in a radial pattern, more node-like in the posterior half of the platform, fusing with the carina at, or very nearly at, its posterior termination; outer trough-like groove short, ending abruptly where outer row of nodes fuses to the carina; inner trough extends nearly the full length of the platform, but generally shallows posteriorly.

In lateral view, the parapets, whether discrete or fused with the carina are high, almost as high as the carina; platform somewhat less high than wide, sides and rear are vertical to slightly overhanging; blade high, highest denticle in anterior one-third.

In aboral view the platform is broadly and deeply excavated with both maxima occurring in the anterior one-third, the outer side is less expanded laterally than the inner, narrow flanges border both sides of the platform, and the entire basal cavity is smaller than in previous species of the lineage; basal cavity extended anteriorly as a groove along the aboral surface of the blade.

Remarks.—The fusion of the outer nodose row and the carina is more anteriorly located in this species than in *Gnathodus* n.sp. B. The degree of fusion is somewhat variable, but the nodose row and carina become progressively more tightly fused posteriorly. For the anterior portion, where the carina and row approach each other, the same remarks apply as for *Gnathodus* n.sp. B. A few specimens of this species show the beginning of the loss of the inner nodose row as well.

Murray and Chronic's specimen fits very well within this

species. Their three specimens figured in oral view and assigned to *Gnathodus roundyi* therefore belong to three different species, *G. n.spp.* A, B, and C according to the classification employed here. In the Allegheny and Pottsville collections such a combination of these three species could be found only in the Putnam Hill and Vanport Members, and their material is probably similar in age.

Material.-Thirty-eight specimens from the Putnam Hill Member, 358 specimens from the Vanport Member, and 9 specimens from the Columbiana Member.

Distribution.-Appalachian occurrences as outlined above, the Minturn Formation of Colorado.

Intermediate gnathodids.

Plate 3, Figures 17, 18.

Gnathodus roundyi Gunnell. Ellison, 1941, p. 138, pl. 23, figs. 23, 25, 26.

Gnathodus sp. Sturgeon & Youngquist, 1949, p. 383, pl. 74, figs. 7, 8.

Description.-Forms intermediate between *Gnathodus n.sp.* C and *G. roundyi* in almost totally lacking the outer nodose row, in retaining scattered nodes from the row, and in showing some reduction in the inner row as well.

Remarks.-These forms are too sparse in the Allegheny to describe formally, but they probably eventually will be described and named as a new species from some other area. These forms are known to dominate some units in the Midcontinent region.

Separating forms such as the one described by Ellison because they possess two, rather than one, outer nodes may seem

overly discriminating, but experience has shown that *Gnathodus roundyi* with its single node is a stable and important morphologic expression of the phylogeny within the genus. Forms between *Gnathodus* n.sp. C, which still maintains a distinct row of nodes, and *G. roundyi* with its single node, should probably be placed in a single, variable, transitional species.

Sturgeon and Youngquist's specimen is from the Columbiana Member as are most of my specimens in this category.

Material.-Thirteen specimens from the Columbiana Member, 1 specimen from the Washingtonville Member.

Distribution.-Appalachian occurrences as listed above, also several units in the Midcontinent, including the Excello Shale and Houx Member as listed by Ellison (1941).

Gnathodus roundyi Gunnell.

Plate 3, Figures 11-16.

Gnathodus roundyi Gunnell, 1931, p. 249, pl. 29, figs. 19, 20;

Ellison, 1941, p. 138, pl. 23, figs. 27, 28 *only*.

Description.-In oral view platform acutely lanceolate, posterior one-half to two-thirds of outer side concave, inner side entirely convex or partly straight partly convex, rarely partly concave, widest in anterior one-third to one-fourth, pointed posteriorly; blade continued posteriorly on platform as a sinuous carina, continuing to the posterior terminus of the platform; outer side of platform moderately expanded in anterior one-third, converging with carina so that posterior two-thirds of outer side of carina marks outer limit of platform, a single conspicuous node located on anterior

expansion of the outer margin of the platform; inner nodose row consists of slightly to greatly laterally elongated nodes arranged in a row which is farthest from the carina in the anterior one-third of the platform, converging abruptly toward the posterior of the platform and commonly disappearing before reaching the posterior end of the carina, either by missing nodes or by fusing with the carina in the posterior one-half of the platform.

In lateral view the carina is the highest element of the platform, the outer node is considerably lower, the inner nodose row slightly lower; platform slightly arched; blade high with the highest denticles in the anterior one-third.

In aboral view the basal cavity considerably elongated, wide and deep, deepest and widest in anterior one-third, bordered by shelf-like flanges.

Remarks.—The label on Gunnell's slide lists "cotypes", but only a single specimen is present. It probably was used for both of his figures and is the same one that Ellison (1941) designated as lectotype.

The single node of the lectotype is a more constant feature for the species than might be supposed. References to this species which lack illustration cannot presently be substantiated or rejected and are therefore omitted.

Material.—One specimen from each of the Putnam Hill and Vanport Members, 209 from the Columbiana Member, and 1 from the Washingtonville Member.

Distribution.—Appalachians as indicated, Midcontinent in several units including the Anna Member (Gunnell) and Excello Shale

(Ellison).

Gnathodus dilatus Stauffer and Plummer.

Plate 3, Figures 3-10.

Gnathodus dilatus Stauffer & Plummer, 1932, p. 40, 41, pl. 4, figs.

10, 11, 13, 14; Fay, 1952, p. 96.

Cavusgnathus sp. Sturgeon & Youngquist, 1949, p. 383, pl. 74, fig.

13.

Description.-In oral view unit slightly to moderately bowed, blade relatively straight; platform elongate, sharply pointed posteriorly, expanded on inner side, only slightly expanded on outer side, resulting in an outer margin parallel to carina and an inner margin diverging from carina anteriorly; blade continued on platform as a nodose carina extending to the posterior tip of the platform, forming most of the outer margin of the platform; some specimens show a shelf-like hump on the anterior portion of the outer side; inner margin of the platform ornamented by a nodose row extending most of the length of the platform, commonly with a few gaps posteriorly and some tendency for the posteriormost nodes to fuse to the carina.

In lateral view, platform high, higher than wide, outer margin vertical, inner margin a nodose parapet somewhat lower than the carina which forms the outer margin; blade has highest denticle in anterior one-third.

In aboral view entire aboral surface of platform excavated, basal cavity decidedly asymmetric, outer side relatively straight, expanded on inner side, deepest and widest in anterior one-third, basal cavity extended anteriorly as a groove along the aboral edge

of the blade.

Remarks.-This species differs from all other gnathodids in this series in lacking all vestiges of ornamentation on the outer side of the platform. Because of the single row of nodes and carina, this species superficially resembles *Cavusgnathus*, which prompted Sturgeon and Youngquist to assign a specimen of it to that genus. The types of nodes present in the two genera are quite distinct and this is evident from their figures.

Material.-One specimen from the Putnam Hill Member, 50 from the Columbiana Member, and 6 from the Washingtonville Member.

Distribution.-Only known from the Allegheny occurrences listed above and the Mineral Wells Formation of Texas.

"Terminal" gnathodids.

Plate 3, Figures 1, 2.

Remarks.-These two specimens are insufficient to warrant a description. It is uncertain that they are even complete, although the platform of one of them appears to be. Both bear a single row of nodes, apparently representing the carina of earlier gnathodids. One (fig. 1) also appears to have a single node flanking this row. These are presently interpreted as representatives of the final episode in gnathodid evolution in which both nodose rows have totally, or almost totally, disappeared, leaving only the carina. Other interpretations of such specimens, perhaps as pathologic individuals, are possible, but until more material is available the matter of the interpretation of these two specimens cannot be resolved.

Material and distribution.-Two specimens from the Washingtonville

Member.

GENUS *IDIOGNATHODUS* GUNNELL, 1931.

Type species: *Idiognathodus claviformis* Gunnell, 1931.

Diagnosis.-Platform conodonts with greatly expanded (gnathodid) basal cavities and oral surfaces ornamented with a series of nodes, transverse ridges, or both. The blade meets the platform near the center of its anterior edge and continues posteriorly some distance as a carina on the platform.

Remarks.-The most distinctive feature of the idiognathodids as a group is the presence of transverse ridges extending across the platform. The type species, *I. claviformis*, does not have continuous ridges, but has nodes and some discontinuous ridges. It probably represents a relatively insignificant offshoot in the evolution of the genus. This genus is separated from the closely allied *Streptognathodus* by the development of these transverse ridges instead of a longitudinal trough. The two genera completely intergrade in various parts of the Pennsylvanian.

In this study a few specimens have been assigned to *Idiognathodus claviformis* and the balance to *I. delicatus*. This practice reflects my current viewpoint that the genus contains no validly defined, phylogenetically sound species. Except for *Idiognathodus claviformis* and its synonyms, all other forms can best be referred to the simplest, most generalized, and equally old species, *I. delicatus*. Accordingly, all forms described since my previous work are listed as synonyms of *I. delicatus*, and all of longer standing, although not listed individually, are also considered

inseparable pending proper evaluation.

Idiognathodus claviformis Gunnell, 1931.

Plate 4, Figures 1-24.

Idiognathodus claviformis Gunnell, 1931, p. 249, 250, pl. 29, fig.

21 (=lectotype); Ellison, 1941, p. 137, pl. 23, figs. 12-17,
19, 20, 22, non figs. 18, 21, 23.

(for additional synonyms see Merrill, 1964, p. 96,97).

Diagnosis.-A robust species of *Idiognathodus* in which all margins of the platform are rounded and whose oral surface is ornamented with nodes and discontinuous ridges.

Remarks.-The lack of continuous ridges is the determinative feature for this species. This condition probably arose in a variety of ways and it is unlikely that the species is strictly monophyletic.

Material.-Approximately 100 specimens from the Allegheny marine units. In the Washingtonville Member many specimens are intermediate between *Idiognathodus* and *Streptognathodus* in the deterioration of the transverse ridges. It is difficult to separate these from specimens of *Idiognathodus claviformis*.

Idiognathodus delicatus Gunnell, 1931.

Plates 5-8, All Figures.

Idiognathodus delicatus Gunnell, 1931, p. 250, pl. 29, figs. 23, 24.

(Ellison, 1941, p. 134, gives a detailed synonymy through 1941).

(Merrill, 1964, p. 73-76, gives a detailed synonymy through 1964).

Post-1964 synonymy:

- Idiognathodus togashii* Igo & Koike, 1964, p. 188, pl. 28, figs. 1-4.
- Idiognathodus acutus* Ellison. Lindström, 1964, p. 114, fig. 43F.
- Idiognathodus cf. acutus* Ellison. Lindström, 1964, p. 174, fig. 63C;
Fúlfaro, 1965, p. 36, pl. 1, fig. H.
- ? *Idiognathodus antiquus* Stauffer & Plummer. Lindström, 1964, p. 60,
fig. 21G, p. 114, fig. 43G.
- Idiognathodus cf. delicatus* Gunnell. Gabert, Stoppel, & Vinken, 1965,
p. 404, pl. 47, fig. 9.
- Idiognathodus aff. I lobatus* Gunnell. Gabert, Stoppel, & Vinken,
1965, p. 404, pl. 47, figs. 4a, b.
- Idiognathodus tersus* Ellison. Gabert, Stoppel, & Vinken, 1965, p.
404, 405, pl. 47, fig. 11.
- ? *Idiognathodus* sp. juv. Gabert, Stoppel, & Vinken, 1965, p. 405,
pl. 47, fig. 12.
- Idiognathodus* sp. A Gabert, Stoppel, & Vinken, 1965, p. 405, pl. 47,
figs. 7a, b.
- Idiognathodus* sp. B Gabert, Stoppel, & Vinken, 1965, p. 405, pl. 47,
fig. 6.
- Idiognathodus* sp. C Gabert, Stoppel, & Vinken, 1965, p. 405, pl. 47,
fig. 8.
- Streptognathodus* sp. Gabert, Stoppel, & Vinken, 1965, p. 406, pl.
47, figs. 10a, b.
- Idiognathodus* sp. cf. *I. magnificus* Stauffer & Plummer. Murray &
Chronic, 1965, p. 601, pl. 71, figs. 7-12.
- Idiognathodus meekerensis* Murray & Chronic, 1965, p. 601, 602, pl.
71, figs. 13-29.

Idiognathodus sp. Fúlfaro, 1965, p. 36, 37, pl. 1, fig. G; Lane, 1967, p. 936, pl. 119, figs. 10, 11.

Idiognathodus humerus Dunn, 1966, p. 1300, 1301, pl. 158, figs. 6, 7.

Idiognathodus incurvus Dunn, 1966, p. 1301, pl. 158, figs. 2, 3.

Streptognathodus anteeccentricus Dunn, 1966, p. 1302, pl. 157, figs. 11, 12.

Streptognathodus parvus Dunn, 1966, p. 1302, 1303, pl. 158, figs. 9, 10; Koike, 1967, p. 305, 306, pl. 2, figs. 13-17 *only*.

Idiognathodus delicatus Gunnell. Koike, 1967, p. 304, 305, pl. 2, figs. 18-23.

Diagnosis.—As used here in a provisional sense, *Idiognathodus delicatus* includes all cross-ridged idiognathodids.

Remarks.—Ten informal morphotypes have been selected to illustrate phylogenetic differences among the Allegheny idiognathodids. Their descriptions will be brief and informal, stressing oral configuration of the platform.

Material.—More than 20,000 specimens.

Idiognathodus delicatus Morphotype α .

Plate 5, Figures 1-3.

Description.—Platform wide in anterior one-third to one-half, tapering abruptly, broadly rounded on outer side and distinctly incurved on inner, acutely rounded posteriorly, twisted slightly out of a plane, inner side higher; inner anterior region occupied by a large, roughly oval nodose lobe, crowded by numerous small regular nodes; outer nodose lobe of roughly equal length, more elongate, crowded with nodes similar to those on the inner lobe; carina short,

one-eighth or less the length of the platform, bordered for its full length by distinct sharp-edged ridges which flare away from it anteriorly and become nodose; a diamond-shaped field of transverse ridges occupies the posterior three-fourths or more of the platform; front of the diamond distinctly shorter than the rear; transverse ridges numerous, fine, slightly sinuous, regular and parallel.

Remarks.-The broadly rounded inner lobe and strong curvature produce a distinctive form that is probably a valid species.

Distribution.-Primarily this is an upper Pottsville form that also occurs rarely in the Putnam Hill Member and even more rarely in the Vanport Member.

Idiognathodus delicatus Morphotype B.

Plate 5, Figures 4-9, Plate 7, Figures 1-3.

Description.-Platform biconvex in oral view, sublanceolate to subfusiform, tapering to a point posteriorly; inner lobe elongate, consisting of one or two longitudinal rows of nodes, forming an oval arc of a relatively few nodes extending from one-third to one-half the length of the platform; outer nodose lobe similar, consisting of one or two rows of nodes extending nearly as far posteriorly as the inner lobe, containing nearly as many nodes as the inner lobe; carina slightly over one-third the length of the platform, may truncate a transverse ridge or two anteriorly, carina may be flanked by an indistinct ridge or ridges or arcuate rows of nodes, convex toward the carina; carina followed posteriorly by a field of transverse ridges, less diamond-shaped than triangular, consisting of several fairly regular, continuous, slightly sinuous ridges.

Remarks.—This morphotype seems most common in the Putnam Hill and Vanport Members. Some specimens show similarities to morphotype α , but they differ in lacking the lateral curvature of that form, in having fewer nodes and ridges, and in overall shape.

Distribution.—All four Allegheny marine units, most common in the lower two.

Idiognathodus delicatus Morphotype γ .

Plate 5, Figures 17-21.

Description.—Platform diamond-shaped in oral view, widest point about one-third of the distance behind the anterior end, platform more than one-third as wide as long, posterior termination of platform pointed; inner lobe large, an elongate oval extending up to half the length of the platform, containing numerous, large, randomly placed nodes; outer lobe similar, narrower, about as long with fewer nodes of about the same size as those of the inner lobe; carina generally short, one-fourth to one-half the length of the platform, flanked by ridges which may either be nodose or rim-like and which in some specimens entirely set off the nodose lobes; field diamond-shaped with numerous, regular, fine transverse ridges, and is widest just posterior of the nodose lobes.

Remarks.—These forms show several characteristics in common with both morphotypes α and β , but lack the regularity of the lobes and the curvature of morphotype α , and have more highly developed lobes and a differently shaped field than morphotype β .

Distribution.—This form has been recognized only from the Putnam Hill Member.

Idiognathodus delicatus Morphotype δ .

Plate 5, Figures 10-16, Plate 7, Figures 14-18.

Description.-In oral view platform lanceolate, inner margin relatively straight, outer margin slightly to strongly convex, resulting in the posterior termination of the platform to usually be pointed inward at a slight to a sharp angle; inner lobe narrow, elongate, bearing one or two rows of small nodes extending to about midlength; outer lobe containing a single row of nodes commonly not extending as far posteriorly as the inner lobe; carina extending to about midlength, not paralleled by conspicuous ridges; field of triangular shape, possessing few ridges, ridges, ridges generally coarse, fairly straight and regular, commonly showing a tendency to break up into nodes, especially along the inner margin.

Remarks.-This is a rather general and loose grouping of forms which show reduction in the development of nodes and ridges, and fairly strong curvature of the platform.

Distribution.-Apparently most common in the Vanport and Columbiana Members; it is also present in the Putnam Hill Member.

Idiognathodus delicatus Morphotype ϵ .

Plate 6, Figures 1-9.

Description.-Platform in oral view lanceolate, posteriorly pointed, platform curved strongly to not at all, usually widest just anterior to midlength; inner lobe a large oval area of irregular nodes and ridges forming random patterns; outer lobe consists of a few nodes along the margin of the platform, carina short, about one-fourth the total length of the platform, parallel ridges where

present do not continue very far onto the platform, field irregularly shaped with ridges commonly present anterior of the terminus of the carina; ridges irregular, sinuous, seldom parallel throughout field, broken, not normal to the long axis of the platform.

Remarks.-These forms virtually lack the outer lobe and have broad areas on both lobes and field covered with irregular nodes and ridges. It differs in these respects from the previously described morphotypes and may give rise to some of the forms assigned to *I. claviformis*.

Distribution.-Probably most common in the Putnam Hill Member, but also present in the Vanport Member.

Idiognathodus delicatus Morphotype 5.

Plate 6, Figures 10-15.

Description.-Platform lanceolate or more commonly wedge-shaped, pointed posteriorly; inner lobe irregularly shaped, oval to lenticular consisting of a flat surface on which are scattered small, pimple-like nodes and a few, fine, irregular ridges; outer lobe poorly developed, bearing a row or two of more regular small nodes; carina continues on platform for about one-third of its length, may have incomplete bordering ridges; field long, generally covering the posterior two-thirds of the platform, consisting of numerous fine, fairly regular ridges.

Remarks.-The better organization of the elements of the ornamentation, especially in the field, along with the smaller size of the nodes on the lobes separate this from the similar morphotype 6. It is similar to, and may prove to be, Ellison's *I. acutus*.

Distribution.—Presently reported from the Vanport and Putnam Hill Members, more common in the former.

Idiognathodus delicatus Morphotype n.

Plate 7, Figures 4-13.

Description.—In oral view platform narrowly lanceolate with moderate inward curvature, straight to slightly concave on inner side, moderately to strongly convex on outer side; inner lobe bears a few nodes in a single row extending not more than one-half the length of the platform; outer lobe poorly developed where present, a few irregular nodes may be present; carina usually one-half to two-thirds the length of the platform, not paralleled by ridges, carina usually truncates several ridges; field extends some distance anteriorly beyond the terminus of the carina with flanking paired half ridges; ridges few, fairly strong, relatively simple and regular.

Remarks.—The reduction of both lobes separates this from previously described morphotypes. It is part of the lineage giving rise to the streptognathodids.

Distribution.—Present in the Columbiana, this morphotype is most common in the Washingtonville Member.

Idiognathodus delicatus Morphotype o.

Plate 8, Figures 1-6.

Description.—Platform in oral view irregularly lanceolate, pointed posteriorly, slightly convex on inner side, strongly so on outer side; inner lobe irregular, large or small, consisting of a variable number of coarse nodes and ridges; outer lobe poorly developed, bearing a few coarse nodes, not well set off from remainder of the

platform; carina moderately long, up to one-half the length of the platform, not paralleled by ridges; field irregularly shaped, covered by a few coarse, irregular transverse ridges which commonly are broken.

Remarks.-Like morphotype η , this morphotype has a strong reduction of the accessory lobes. It is also distinguished by its extremely coarse ornamentation which is also more irregular.

Distribution.-Present in the Columbiana, most common in the Washingtonville Member.

Idiognathodus delicatus Morphotype 1.

Plate 8, Figures 7-12.

Description.-Platform in oral view sublanceolate, pointed posteriorly, varies from slightly to strongly curved; inner lobe prominent, but bears few nodes, commonly arranged in a single row less than one-half the length of the platform; outer lobe not distinctly set off from field, poorly developed, containing at most a few nodes; carina extends onto platform for about one-third of its length, bordered by short ridges; field occupied by transverse ridges, commonly broken, so that a central portion of each original ridge is aligned with the carina.

Remarks.-This morphotype differs from the preceding one in having greater regularity of its nodes and ridges, a moderately developed carina, but with some of the ridges behind the carina being broken. This morphotype may be part of the lineage leading to *Streptognathodus*.

Distribution.-Columbiana and Washingtonville Members have yielded this form, although possibly present in other units as well.

Idiognathodus delicatus Morphotype κ.

Plate 8, Figures 17-22.

Description.-Platform in oral view lanceolate, nearly symmetrical, only slightly curved laterally, acutely pointed posteriorly; inner lobe usually well developed, occupied by small, distinct, regular nodes, not well organized into rows, lobe extending up to one-half the length of the platform; outer lobe well to poorly developed, similar in character to, but smaller than, the inner lobe; carina extends onto platform at least to midlength, truncates several transverse ridges, flanked by rows of nodes which are continuous with each accessory lobe; field small, triangular, confined to posterior one-third of platform; transverse ridges few, regular, but commonly broken in the central portion in line with the posterior projection of the carina.

Remarks.-This form maintains fairly good accessory lobes, but the field of transverse ridges shows the effect of the lengthening of the carina in that the ridges are breaking up behind the carina to accomodate it.

Distribution.-This morphotype is definitely ancestral to much of the *Streptognathodus cancellosus* lineage in the upper Allegheny and lower Conemaugh. It has the longest carinae of any forms I have assigned to *Idiognathodus*.

Idiognathodus delicatus Morphotype unassigned.

Plate 6, Figures 16-20, Plate 8, Figures 13-16.

Remarks.-A few specimens, not assigned to morphotypes, are also illustrated.

Distribution.—The same as for the species.

GENUS *STREPTOGNATHODUS* STAUFFER AND PLUMMER, 1932.

Type species: *Streptognathodus excelsus* Stauffer and Plummer, 1932.

Diagnosis.—Platform conodonts with greatly expanded (gnathodid) basal cavities and longitudinal troughs on their oral surfaces, the anterior part of the troughs is occupied by a carina continuous with the blade.

Remarks.—The change from predominantly cross-ridged to predominantly longitudinally troughed forms marks the evolutionary transition from *Idiognathodus* to *Streptognathodus*, a transition which begins and is important in the upper Allegheny rocks, but which continues into the lower Conemaugh. This transition does not take place in a single stratigraphic unit, but rather becomes increasingly conspicuous in succeeding units until the idiognathodids have been entirely replaced by the streptognathodids in higher Conemaugh rocks.

Because the differences between these two genera are in reality so slight, there are numerous intermediate forms difficult to assign with certainty, and the resulting spectrum of variation has somewhat arbitrary divisions.

The ancestor to the common idiognathodids was also a streptognathodid. As a result, many idiognathodids go through streptognathodid growth stages and most of the specimens assigned to *Streptognathodus* from rocks reflecting the hemera of *Idiognathodus*, although morphologically like streptognathodids, are immature specimens of *Idiognathodus*.

Streptognathodus cancellosus (Gunnell, 1933).

Plate 9, Figures 1-13.

Idiognathodus cancellosus Gunnell, 1933, p. 270, pl. 31, fig. 10.

Streptognathodus strigillatus Gunnell, 1933, p. 283, pl. 33, fig. 2.

Idiognathodus biliratus Gunnell, 1933, p. 276, pl. 31, fig. 59.

Idiognathodus binodosus Gunnell, 1933, p. 274, pl. 31, fig. 35.

Idiognathodus confragus Gunnell, 1933, p. 275, pl. 31, fig. 43.

Idiognathodus rugulatus Gunnell, 1933, p. 272, pl. 31, fig. 24.

Idiognathodus simplex Gunnell, 1933, p. 277, 278, pl. 32, fig. 19.

Idiognathodus symmetricus Gunnell, 1933, p. 276, pl. 32, fig. 3.

Streptognathodus cancellosus (Gunnell). Ellison, 1941, p. 131,

132, pl. 22, figs. 23, 26; _____ & Graves, 1941, p. 3, pl.

3, fig. 18; Branson, 1944, p. 309, 327, pl. 46, figs. 23, 26;

Rhodes, 1952, p. 894, pl. 127, fig. 9; Fay, 1952, p. 190;

Stone, 1959, p. 157, 158, text-fig. 4.

Idiognathodus regulatus Gunnell. Ellison, 1941, p. 131 (*lapsus pro rugulatus*).

? *Streptognathodus irregularis* Ellison & Graves, 1941, p. 3, 11, pl.

3, figs. 17, 21, 24; Stone, 1959, p. 158, text-fig. 2.

Streptognathodus ornatus Youngquist & Downs, 1949, p. 170, pl. 30,

figs. 28, 29; Stone, 1959, p. 158, text-fig. 21.

Idiognathodus rectus Youngquist & Downs, 1949, p. 167, 168, pl. 30,

figs. 21-23.

Idiognathodus sp. Sturgeon & Youngquist, 1949, p. 384, pl. 75, fig.

9 only

Idiognathodus delicatus Gunnell. McLaughlin, 1952, p. 619, pl. 83,

fig. 10 only.

Idiognathodus claviformis Gunnell. Rhodes, 1952, p. 889, pl. 127,
fig. 24.

Idiognathodus acutus Ellison. Jennings, 1959, p. 996, pl. 124, fig. 3.

Idiognathodus magnificus Stauffer & Plummer. Clarke, 1960, p. 28,
pl. 51, fig. 2 only.

Streptognathodus oppletus Ellison. Omara & Kenawy, 1966, p. 77-79,
pl. 11, figs. 8, 9.

Description.- In lateral view, platform slightly arched, equal to or longer than blade; blade relatively short and stubby, with up to 10 or more denticles fused nearly to their apices, the highest being located within the first two or three from the anterior end.

In oral view platform long, lanceolate, generally pointed posteriorly; surface of platform concave orally and marked on most specimens by several complete transverse ridges on the posterior part of the platform, the number and degree of completeness varying from specimen to specimen; carina long, truncating many of the transverse ridges, usually abutting posteriorly against the first complete transverse ridge or may be continued posteriorly as a row of nodes in line with the carina and the transverse ridges; trough narrow, shallow, rudimentary; in some specimens nearly entire platform surface is nodose, resembling *Idiognathodus claviformis*; narrow nodose accessory lobes present on both sides of the platform, consisting of from 1 to 15 individual nodes.

In aboral view, little different from most other idiognathodids and streptognathodids, having deeply excavated, flaring basal cavities, deepest in the anterior one-third of the platform.

Remarks.—This species is both a morphologic and phylogenetic descendant of *Idiognathodus delicatus*. It is, in fact, only separated from that species by having a more continuous and extensive trough, and there are numerous individuals difficult to assign because they effectively bridge the morphologic gap between the genera. *Streptognathodus cancellosus* probably arises from more than one of the morphotypes listed for *Idiognathodus delicatus*, morphotypes η , ι , and κ seem most likely ancestors.

The separation of this species from *Streptognathodus oppletus*, according to its author, is based on that species having fewer than two accessory lobes. Although this is another example of a purely arbitrary criterion being employed to separate specimens having close genetic affinities, this one seems to have theoretical soundness as well as practical application. There is phylogenetic significance in the number of accessory lobes. Most of the early streptognathodids in upper Allegheny rocks are bilobate, and in younger faunas of the lower Conemaugh, a shift begins toward monolobate and non-lobate forms. These pass in turn into forms in which the transverse ridges have, for all practical purposes, entirely disappeared, and then into the *Streptognathodus gracilis* (monolobate)–*Streptognathodus excelsus* (bilobate) series of variations. The bilobate transitional forms, presently assigned to *S. cancellosus* are therefore distinguished from other bilobate streptognathodids (especially *S. excelsus*, the type species) in that they retain vestiges of the idiognathodid transverse ridges posteriorly. They are worth separating from closely related monolobate or non-lobate transitional forms in that their epibole does not coincide with those of the simpler forms (Merrill, 1964).

Distribution.—In the context defined above, this species can be separated morphologically from others in lower Allegheny rocks. Because many of those others, similar in morphology, are in reality, probably juveniles of some species of *Idiognathodus*, no attempt has been made to separate these older faunas. The Allegheny range of *Streptognathodus cancellosus*, as treated herein, includes only specimens from the Columbiana and Washingtonville Members, the latter having the greater number of individuals. In the overlying Conemaugh, it is the most abundant platform species in the Lower Brush Creek Member, remains common in the Upper Brush Creek Member, and can be recognized in the Cambridge and Portersville Members. It does not range higher. It has been reported from Desmoinesian and Missourian rocks of Missouri and Kansas, the McLeansboro Group of Illinois, the Glen Eyrie Formation of Colorado, Desmoinesian rocks of Iowa, Minnelusa Formation of South Dakota, Upper Carboniferous limestones in Scotland and Egypt.

Streptognathodus oppletus Ellison, 1941.

Plate 9, Figures 14-25.

Idiognathodus multinodosus Gunnell, 1933, p. 279, pl. 33, fig. 8.

non Streptognathodus multinodosus Gunnell, 1933, p. 280, 281, pl.

32, fig. 11.

? *Streptognathodus cariniferus* Gunnell, 1933, p. 276, pl. 33, fig. 52.

Streptognathodus oppletus Ellison, 1941, p. 132, pl. 22, figs. 13,

14, 16; Branson, 1944, p. 309, 327, pl. 45, figs. 13, 14,

16; Cooper, 1947, p. 269; Fay, 1952, p. 192; Stone, 1959,

p. 157, 158, text-fig. 12.

Streptognathodus mucronatus Youngquist & Downs, 1949, p. 170, pl.

31, figs. 6, 7.

Idiognathodus spp. Sturgeon & Youngquist, 1949, p. 384, pl. 74, figs.

17, 18, 21, 22 only.

Streptognathodus cf. *S. oppletus* Ellison. Rhodes, 1952, p. 894, pl.

127, fig. 18.

non *Streptognathodus oppletus* Ellison. Omara & Kenawy, 1966, p. 77-

79, pl. 11, figs. 8, 9.

Streptognathodus angustus Dunn, 1966, p. 1302, pl. 158, figs. 11-

13.

Description.-In lateral view much like either *Streptognathodus elegnatulus* (with no lobe) or *S. gracilis* (with inner accessory lobe).

In oral view, platform long, lanceolate, posteriorly pointed; carina moderately long, more than one-half the length of the platform, nodose or more commonly ridge-like; rudimentary trough narrow, shallow, several transverse ridges with concave upper edges are present in posterior half of the platform; many specimens have a nodose inner accessory lobe commonly consisting of a single node as is also true of *S. gracilis*; others have laterally and orally flaring parapets in the anterior part of the platform, herein called "frills" as a translation of the German term "*Krause*"; frill usually on inner side of platform only, but may be present on both sides for which the German word "*Kragen*" is more appropriate, literally "collar" (because of a resemblance to the frilled collar worn by medieval knights- Ziegler, personal communication, 1963); frills and collars

are found to some extent in both *Idiognathodus tersus* and *Streptognathodus cancellosus*, but are best developed in *S. oppletus*.

In aboral view unit is indistinguishable from other species of the genus (*inter alia* *Streptognathodus elegantulus*) except that lobate forms may show a slight asymmetry as is present in *S. gracilis*.

Remarks.—This species has either no accessory lobes or a single one on the inner side of the platform. It differs from other streptognathodids in this character in conjunction with being transitional to *Idiognathodus*, evolving from *I. delicatus* in much the same manner as *S. cancellosus*. The frills and collars mentioned in the description are considerably more common in specimens from the lower Conemaugh than from the upper Allegheny. Allegheny specimens also tend to have more nodes on the accessory lobe when present.

Distribution.—Increases in abundance along with *S. cancellosus* from the Columbiana to the Washingtonville Members, although more slowly than that species. Common in the Lower Brush Creek Member, this species reaches its maximum abundance in the Upper Brush Creek Member, and is less common higher in the section, although a specimen or two from the Ames Member has been tentatively assigned to it. Reported from Desmoinesian and Missourian strata of the Midcontinent, Illinois, Iowa, and somewhat older strata (Morrowan) of Nevada.

Streptognathodus spp.

Plate 9, Figures 26-49.

Remarks.—Based on the premise that nearly all conodonts of streptognathodid morphology from the lower Allegheny are merely growth stages of *Idiognathodus*, these forms have not been divided into species

and can conveniently be thought of as immature specimens of *Idiognathodus delicatus*. For most specimens this undoubtedly is true; however, a few of them, for example, pl. 9, figs. 28, 31, 34, 45, and 47, seem to be mature enough to carry the adult characteristics and therefore probably belong to *Streptognathodus* in the strict sense. Plate 9, fig. 31 is a better *Streptognathodus cancellosus* than most of those from the Columbiana and Washingtonville Members. Despite these exceptions, the majority of these individuals illustrated on plate 9, figures 26-49, had they grown to maturity, would be referred to *Idiognathodus delicatus* as ample ontogenetic suites demonstrate. Because it is impossible to tell which individuals would have developed the morphology of one genus or the other during ontogeny, the generic affinities of these individuals cannot be ascertained. Consequently they are placed in the genus whose morphology they possessed upon death, but without specific assignment.

Distribution.-Wherever the adult platform is an idiognathodid similar to *I. delicatus*, growth stages similar to the ones illustrated are encountered. They are likewise present where *Streptognathodus* is the dominant platform conodont, and indeed, the juveniles from the two faunas are indistinguishable. Therefore, the range of this material is essentially "Pennsylvanian, worldwide", although certain stratigraphic units will probably contain somewhat different growth stages.

P L A T E S 1 T H R O U G H 9

The internal organization of the plates is somewhat unusual, but conforms to the notion of providing as much information as possible on the plate itself. The figures are oriented with anterior toward the top of the plate and white lines separate taxa and stratigraphic units. Wide, solid lines separate stratigraphic units; whereas, narrower, solid lines separate species. Narrow, broken lines separate morphotypes within a species.

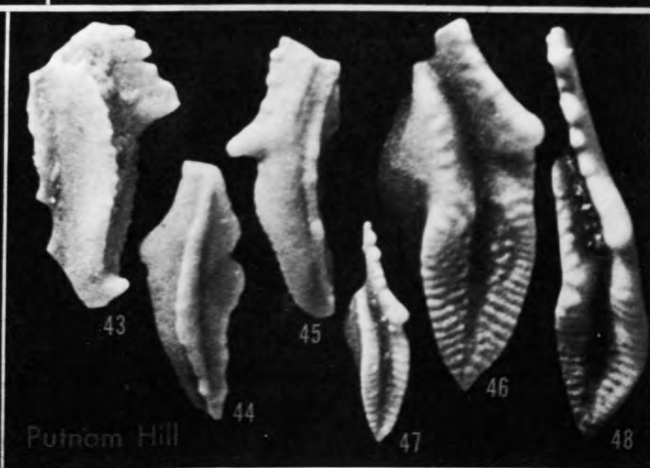
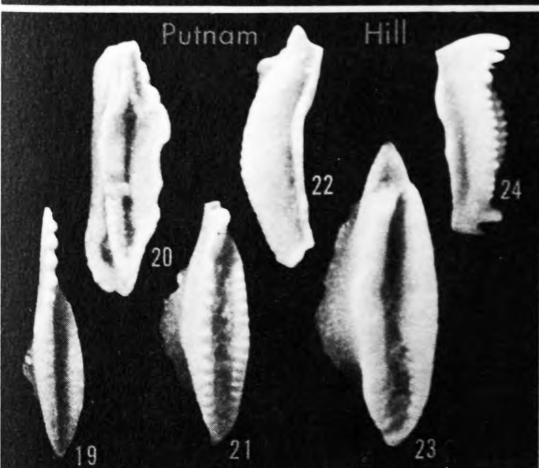
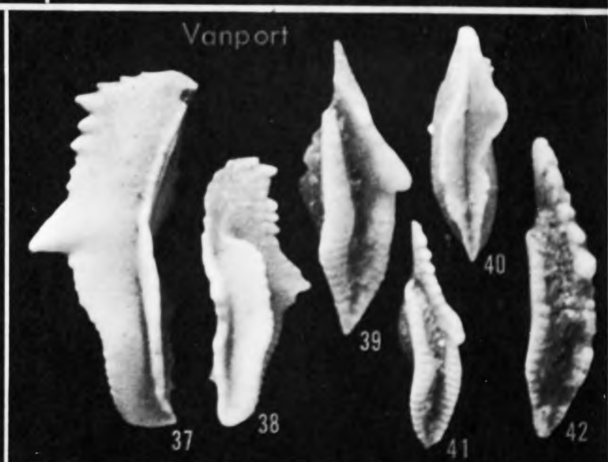
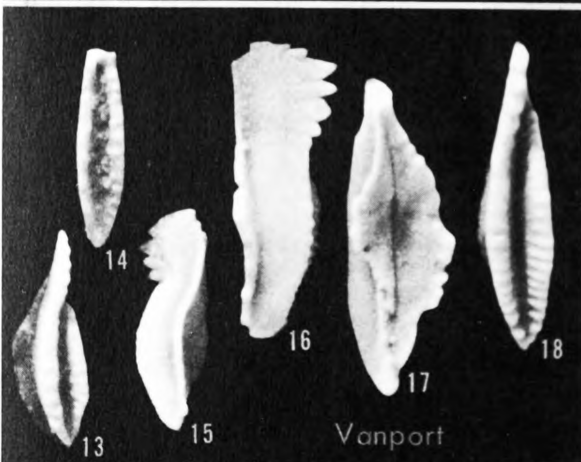
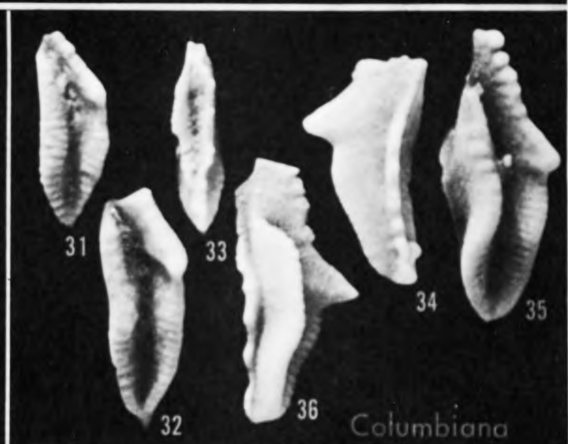
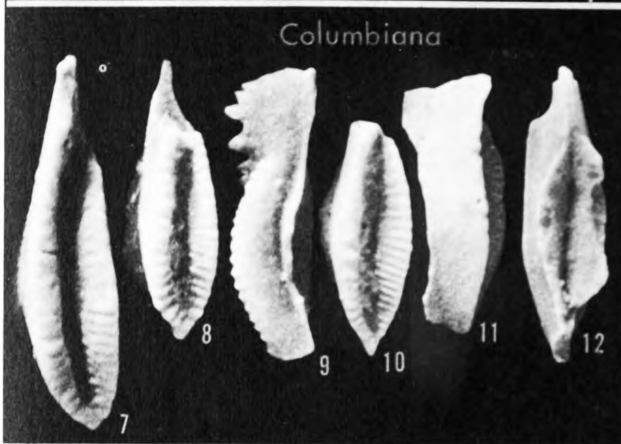
EXPLANATION OF PLATE 1.

CAVUSGNATHUS

all figures $\times 40$

Figures 1-24--*Cavusgnathus lautus*, figures 1,4,5,7,8,10,13,14,18, 19,21,23 are oral views; 2,9,15,22 are inner lateral views; 3,11,16,24 are outer lateral views; 6,12,17,20 are aboral views. Washingtonville localities: figures 1,2-18; 3,4-13; 5,6-9; Columbiana localities: figures 7-5; 8, 9-2; 10-12-4; Vanport localities: figure 13-20; 14-7; 15-18-24; Putnam Hill localities: figure 19-12; 20-23-11; 24-1.

Figures 25-48--*Cavusgnathus gigantus*, figures 25,27,28,31,32,35,39, 41,42,46-48 are oral views; 30,36,38,43 are inner lateral views; 26,34,37, 45 are outer lateral views; 29,33,40,44 are aboral views. Washingtonville localities: figure 25-26;26,27-9; 28,29-13; 30-18; Columbiana localities: figures 31,32-4; 33-35-5; 36-2; Vanport localities: figures 37-40-24; 41-20; 42-7; Putnam Hill localities: figures 43-46-11; 47-1; 48-12.



EXPLANATION OF PLATE 2.

GNATHODUS

all figures $\times 40$

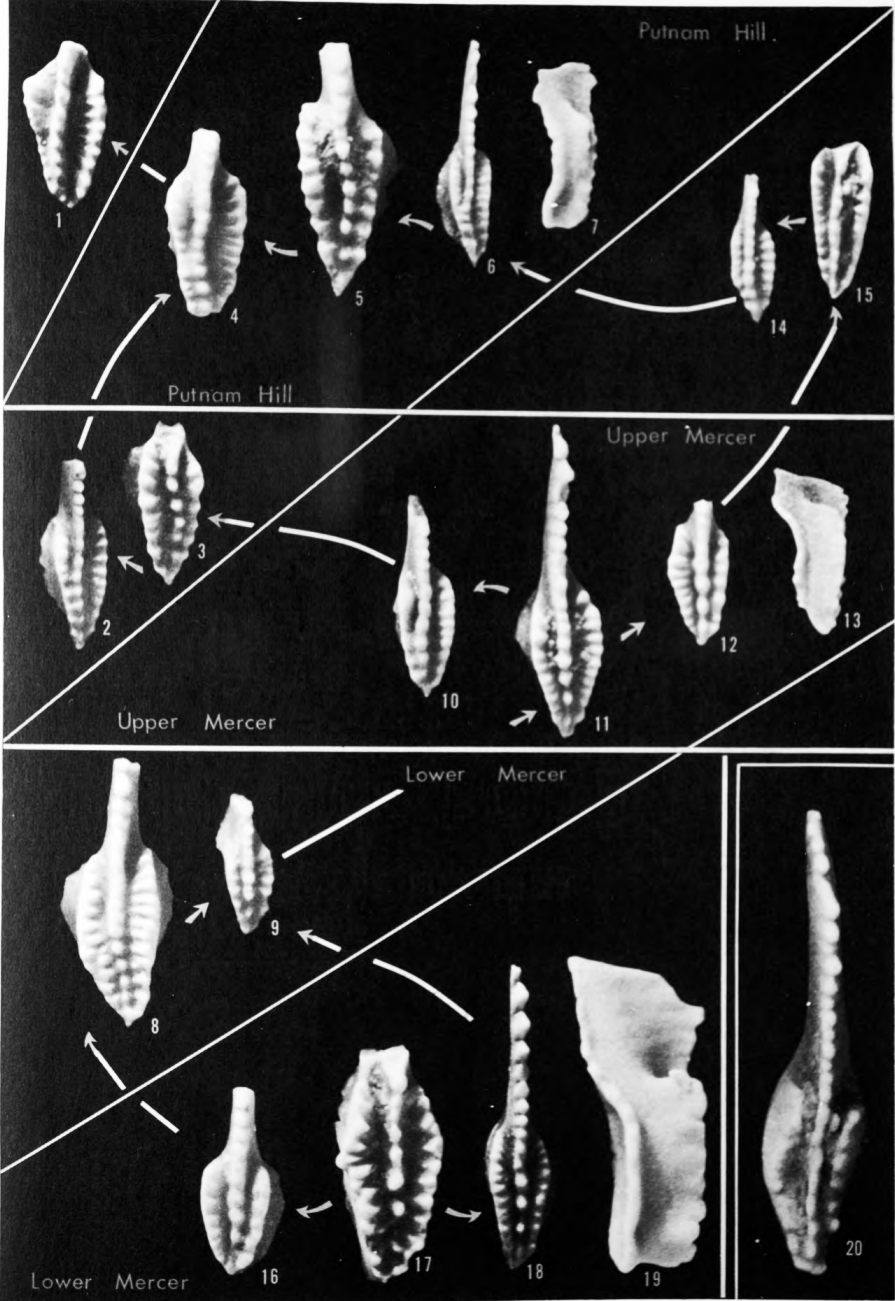
Figure 1--*Gnathodus* n.sp. C, oral view, Putnam Hill locality 19.

Figures 2-7--*Gnathodus* n.sp. B, figures 2-6 are oral views; 7 an outer lateral view. Putnam Hill localities: figure 4-11; 5-20; 6-27; 7-28; Upper Mercer locality: figures 2,3-6.

Figures 8-15--*Gnathodus* n.sp. A, figures 8-12,14,15 are oral views; 13 an outer lateral view. Putnam Hill localities: figure 14-6; 15-22; Upper Mercer localities: figures 10,13-6; 11,12-8; Lower Mercer localities: figures 8-2; 9-4.

Figures 16-19--*Gnathodus bassleri*, figures 16-18 are oral views, figure 19 is an inner lateral view. Lower Mercer localities: figures 16, 17-9; 18-10; 19-2.

Figure 20--*Gnathodus websteri*, oral view of holotype from "early Pennsylvanian" shale near Knoxville, Iowa.



EXPLANATION OF PLATE 3.

GNATHODUS

all figures $\times 40$

Figures 1-2--"Terminal" gnathodids, oral views of two specimens from Washingtonville localities 2 and 13, respectively.

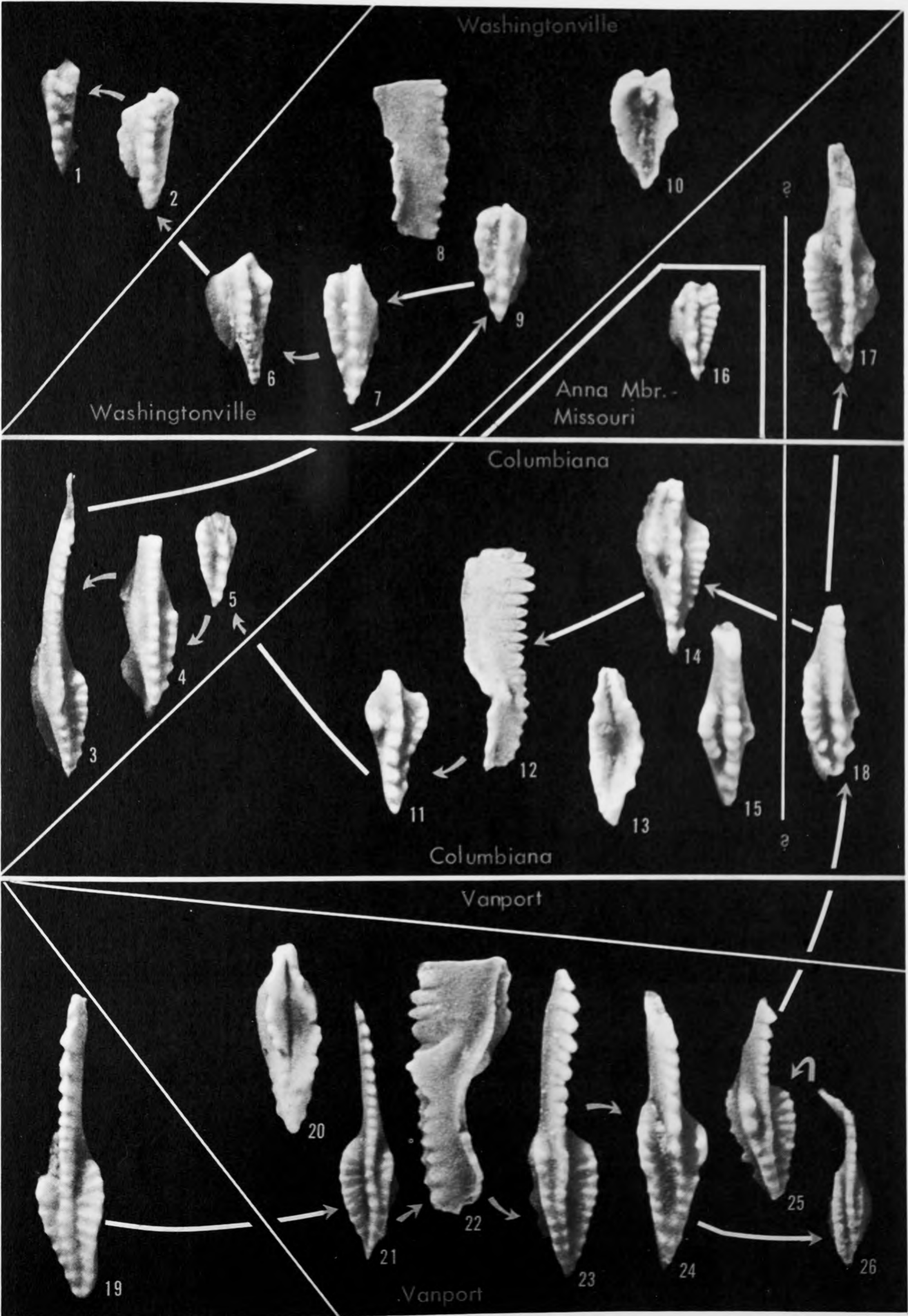
Figures 3-10--*Gnathodus dilatatus*, figures 3-5, oral views of three specimens from Columbiana localities 20, 13, and 5, respectively; figures 6, 7, 9, are oral views of three specimens from Washingtonville localities 13, 9, and 9, respectively; figure 8 is an outer lateral view from Washingtonville locality 23; figure 10 is an aboral view from Washingtonville locality 22.

Figures 11-16--*Gnathodus roundyi*, figures 11, 14, 15 are oral views of three specimens from Columbiana localities 4, 10, and 20, respectively; figure 12 is an outer lateral view from Columbiana locality 20; figure 13 is an aboral view, Columbiana locality 10; figure 16 is an oral view of a topotype from Gunnell's locality.

Figures 17-18--Intermediate gnathodids, oral views of specimens from Washingtonville locality 22 and Columbiana locality 10, respectively.

Figure 19--*Gnathodus* n.sp. B, oral view of a specimen from Vanport locality 36.

Figures 20-26--*Gnathodus* n.sp. C, figures 21, 23-26 are oral views, 20 an aboral view, 22 an outer lateral view. Vanport localities: figures 20, 25-4; 21-23; 22, 24-7; 23-36; 26-22.

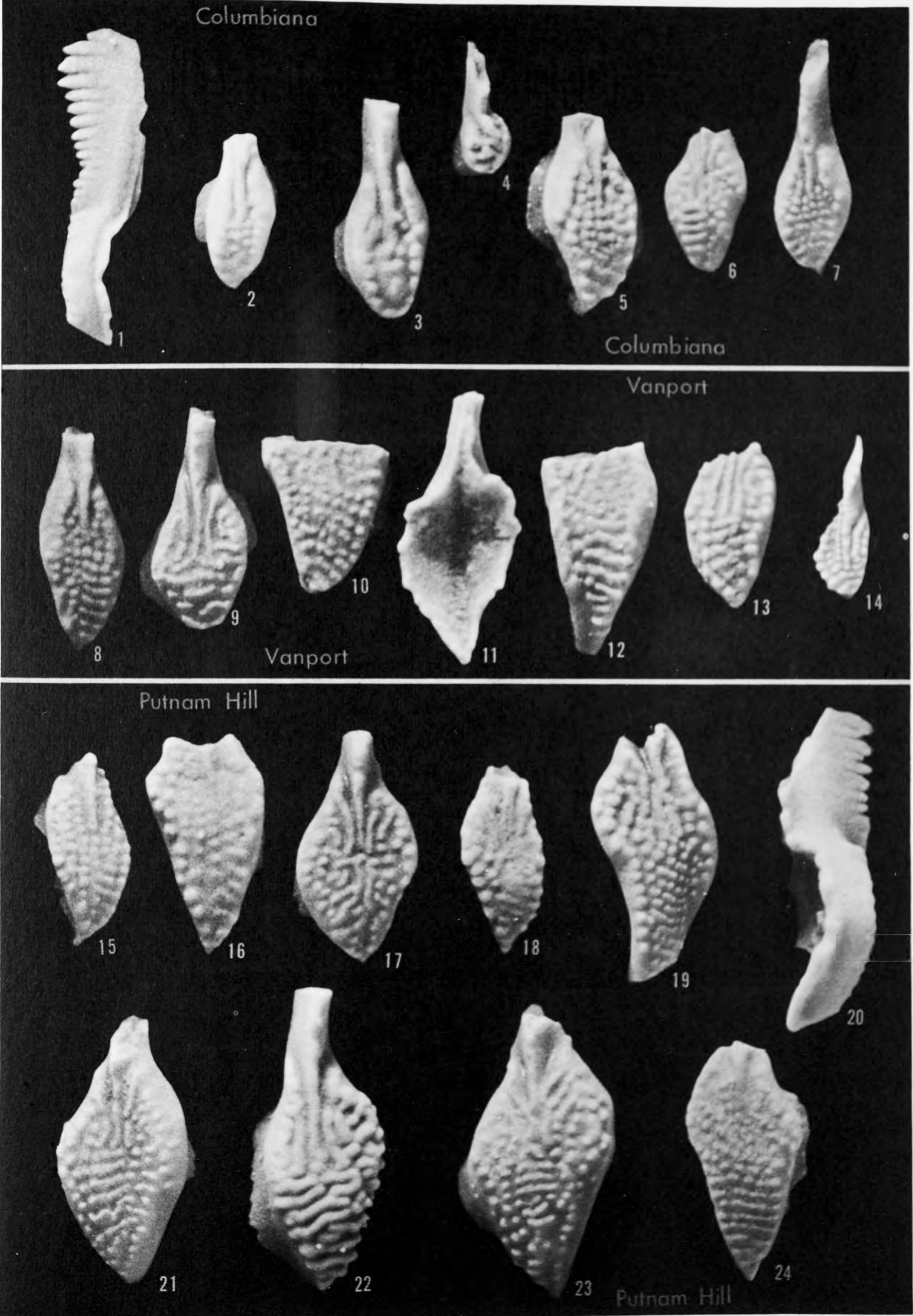


EXPLANATION OF PLATE 4.

IDIOGNATHODUS CLAVIFORMIS

all figures $\times 40$

Figures 1-24--*Idiognathodus claviformis*, figures 2-10, 12-19, 21-24 are oral views, figures 1 and 20 are lateral views, figure 11 is an aboral view. Columbiana localities: figures 1-4; 7-20; 5-13; 6-9; Vanport localities figures 8,13-36; 9-12-7; 14-4; Putnam Hill localities: figures 15,18-11; 16-10; 17,20-22; 19-23; 21,24-20; 22-2; 23-3.



EXPLANATION OF PLATE 5.

IDIOGNATHODUS DELICATUS

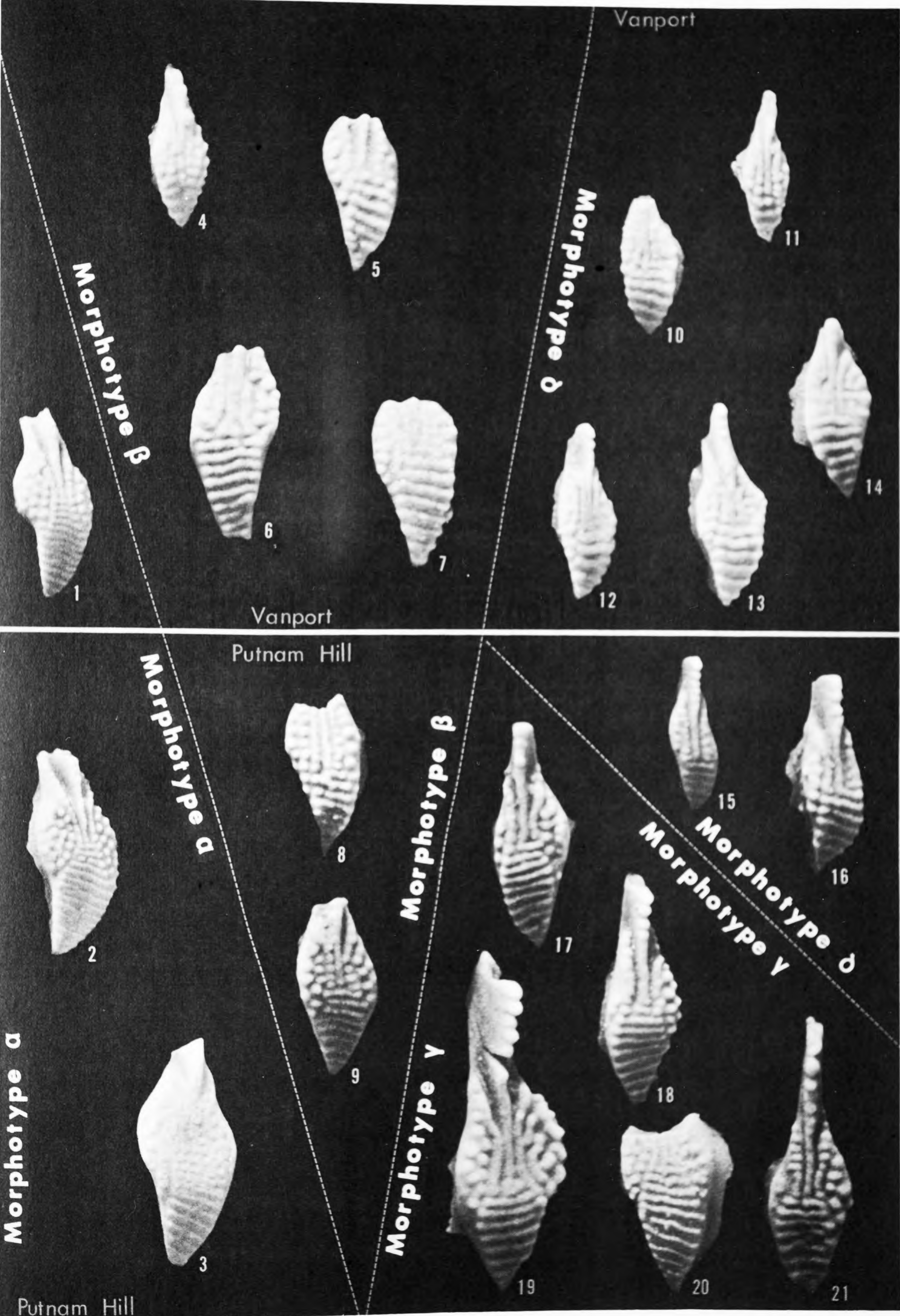
all figures $\times 40$

Figures 1-3--*Idiognathodus delicatus* Morphotype α , all oral views, figure 1 Vanport locality 34; 2,3 Putnam Hill localities 23 and 20, respectively.

Figures 4-9--*Idiognathodus delicatus* Morphotype β , all oral views, figures 4-7 from Vanport localities 23,34,34, and 4, respectively; 8,9 from Putnam Hill localities 3 and 28, respectively.

Figures 10-16--*Idiognathodus delicatus* Morphotype δ , all oral views, figures 10-14 from Vanport localities 23,4,4,4, and 23, respectively; 15, 16 from Putnam Hill localities 4 and 11, respectively.

Figures 17-21--*Idiognathodus delicatus* Morphotype γ , all oral views, Putnam Hill localities: 28,4,3,20, and 28, respectively.



EXPLANATION OF PLATE 6.

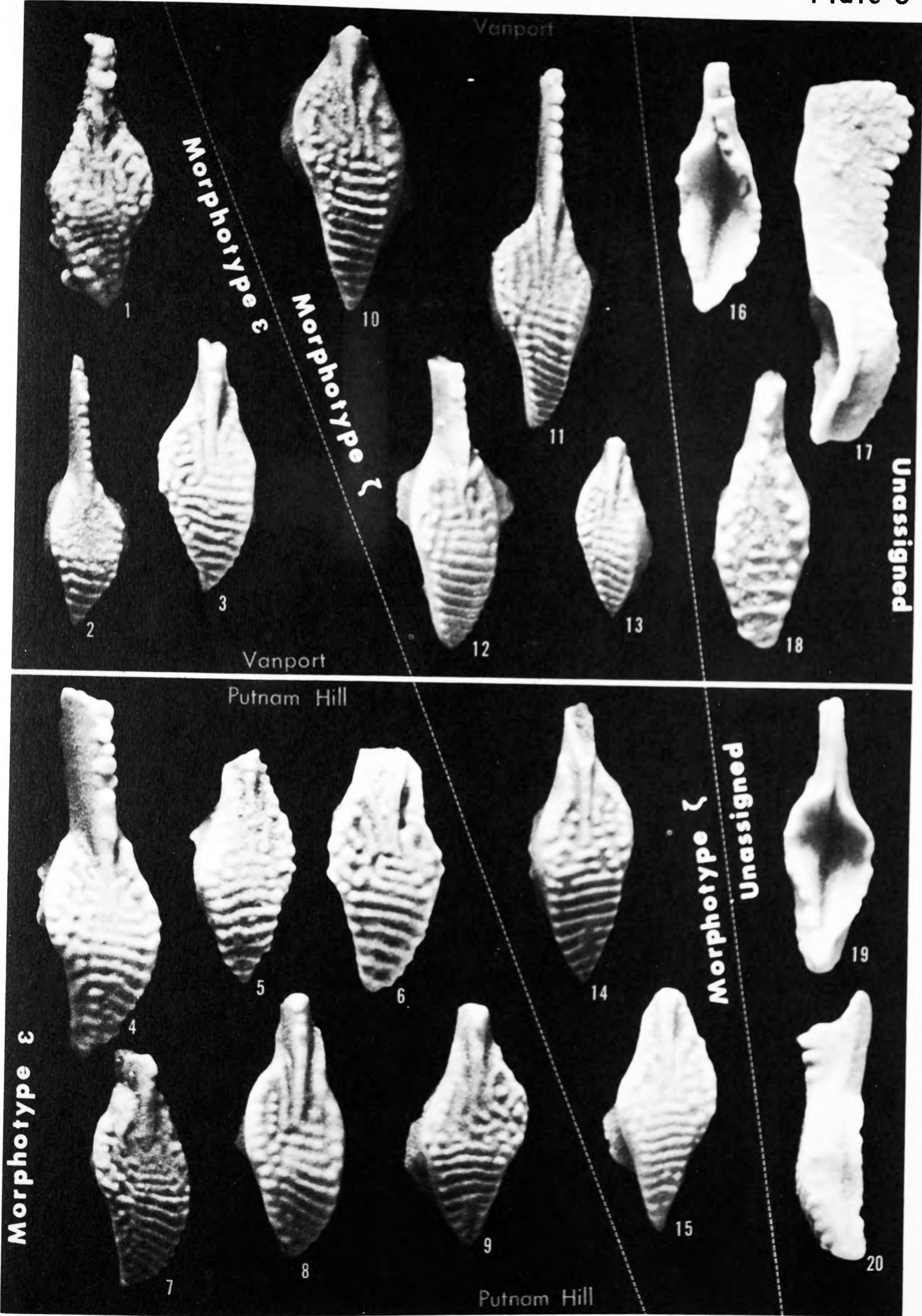
IDIOGNATHODUS DELICATUS

all figures $\times 40$

Figures 1-9--*Idiognathodus delicatus* Morphotype ϵ , all oral views, figures 1-3, from Vanport localities 36,23, and 7, respectively; 4-9 from Putnam Hill localities 23,23,4,4,3, and 20, respectively.

Figures 10-15--*Idiognathodus delicatus* Morphotype ζ , all oral views, figures 10-13 from Vanport localities 7,7,7, and 34, respectively; 14,15, from Putnam Hill localities 20 and 23, respectively.

Figures 16-20--*Idiognathodus delicatus* Morphotype unassigned, figures 16-18, aboral, inner lateral and oral views of three specimens from Vanport locality 36; 19,20 aboral and lateral views of two specimens from Putnam Hill locality 11.



EXPLANATION OF PLATE 7.

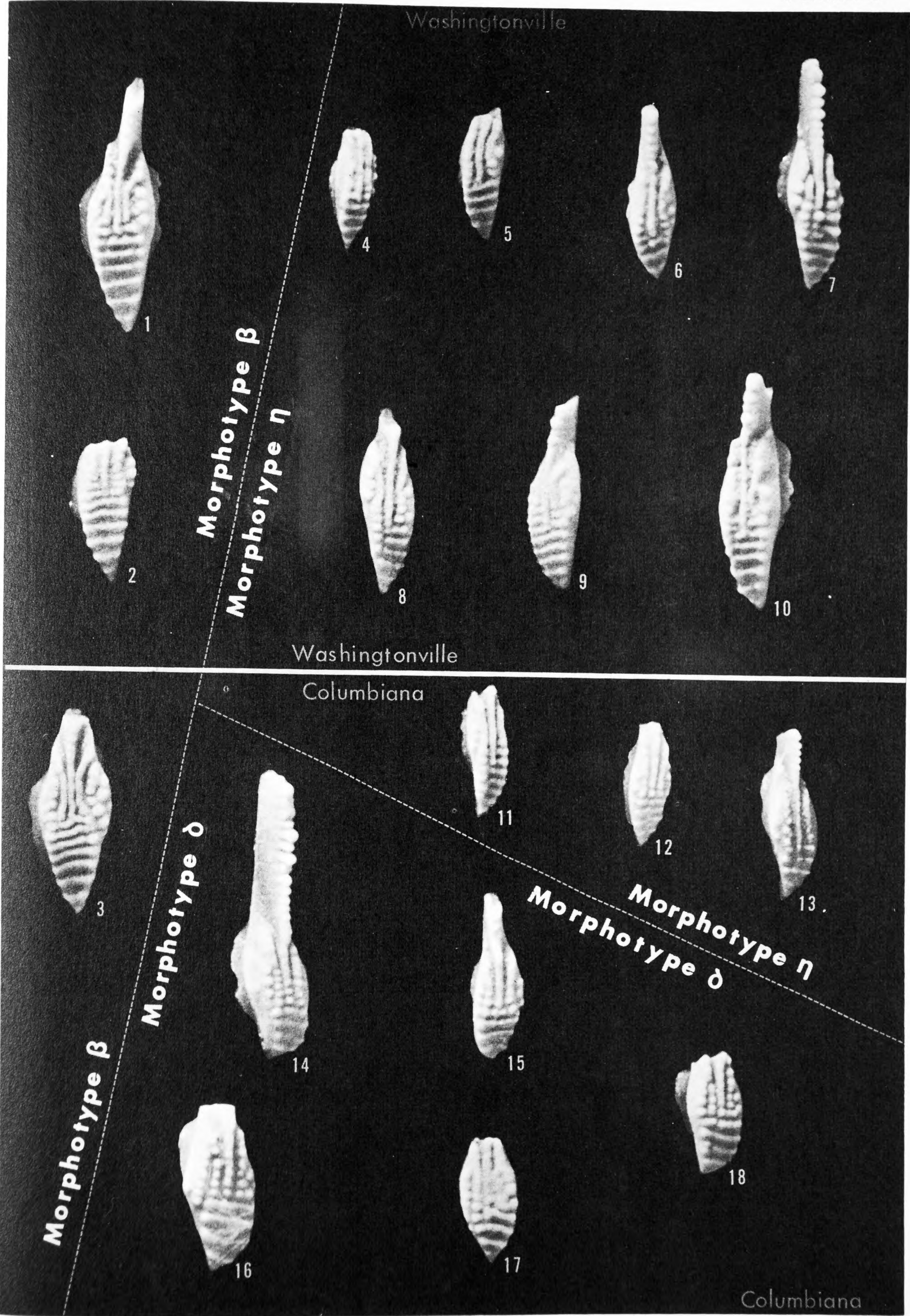
IDIOGNATHODUS DELICATUS

all figures $\times 40$

Figures 1-3--*Idiognathodus delicatus* Morphotype β , all oral views, figures 1,2 from Washingtonville localities 19 and 22, respectively; 3 from Columbiana locality 10.

Figures 4-13--*Idiognathodus delicatus* Morphotype η , all oral views, figures 4-10 from Washingtonville localities 22,13,22,8,22,22, and 19, respectively; 11-13 from Columbiana localities 20,10, and 7, respectively.

Figures 14-18--*Idiognathodus delicatus* Morphotype δ , oral views from Columbiana localities 20,10,7,5, and 5, respectively.



EXPLANATION OF PLATE 8.

IDIognathodus DELICATUS

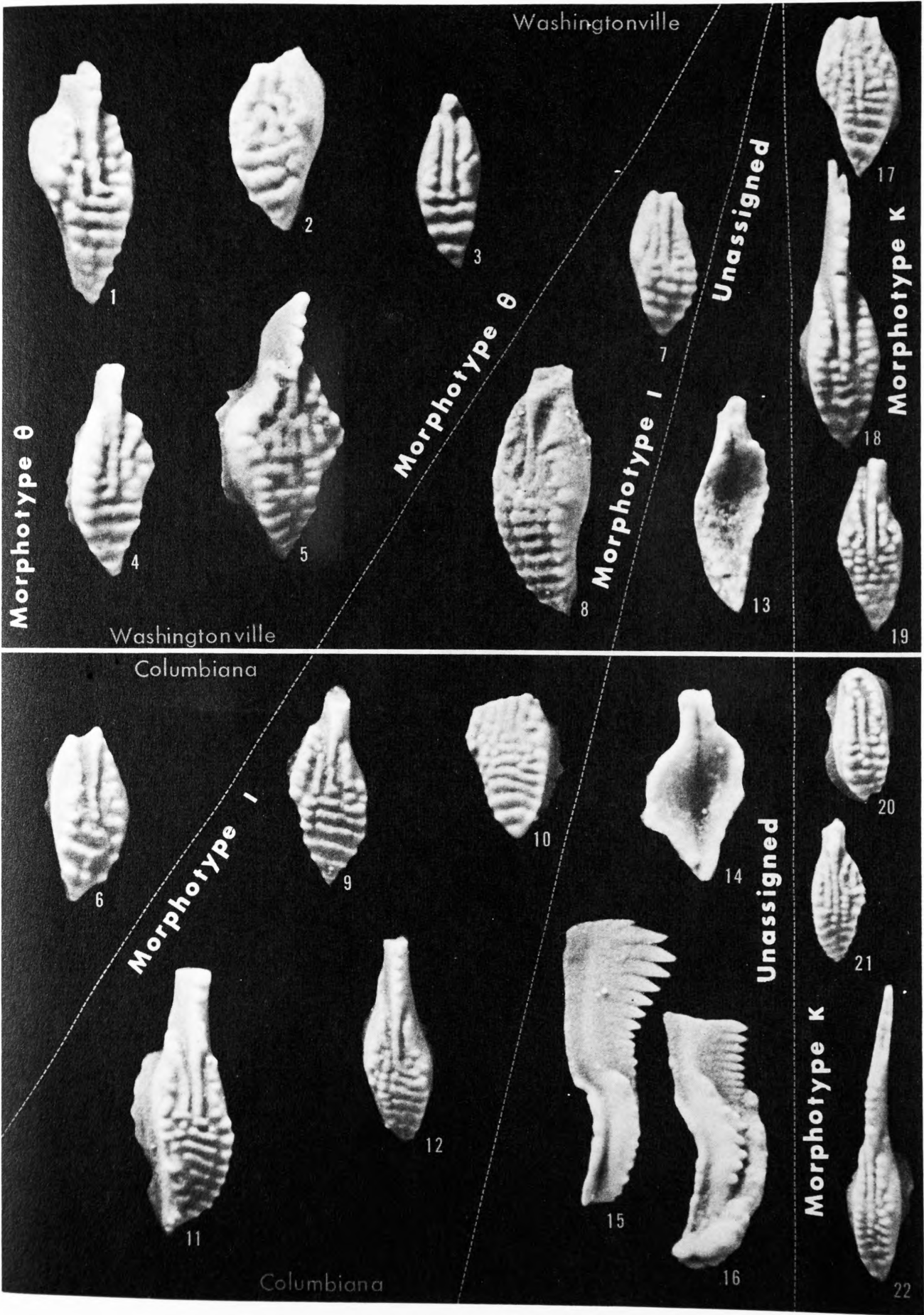
all figures $\times 40$

Figures 1-6--*Idiognathodus delicatus* Morphotype 0, all oral views, figures 1-5 from Washingtonville localities 8,13,8,13, and 13, respectively; 6 from Columbiana locality 7.

Figures 7-12--*Idiognathodus delicatus* Morphotype 1, all oral views, figures 7,8 from Washingtonville localities 13 and 19, respectively; 9-12 from Columbiana localities 7,5,20, and 10, respectively.

Figures 13-16--*Idiognathodus delicatus* Morphotype unassigned, figure 13 aboral view, Washingtonville locality 19; 14 aboral view from Columbiana locality 20; 15, 16 lateral views from Columbiana localities 20 and 7 (with attached foraminifer).

Figures 17-22--*Idiognathodus delicatus* Morphotype 2, all oral views, figures 17-19 from Washingtonville localities 19,8, and 8, respectively; 20-22 from Columbiana localities 5,5, and 10, respectively.



EXPLANATION OF PLATE 9.

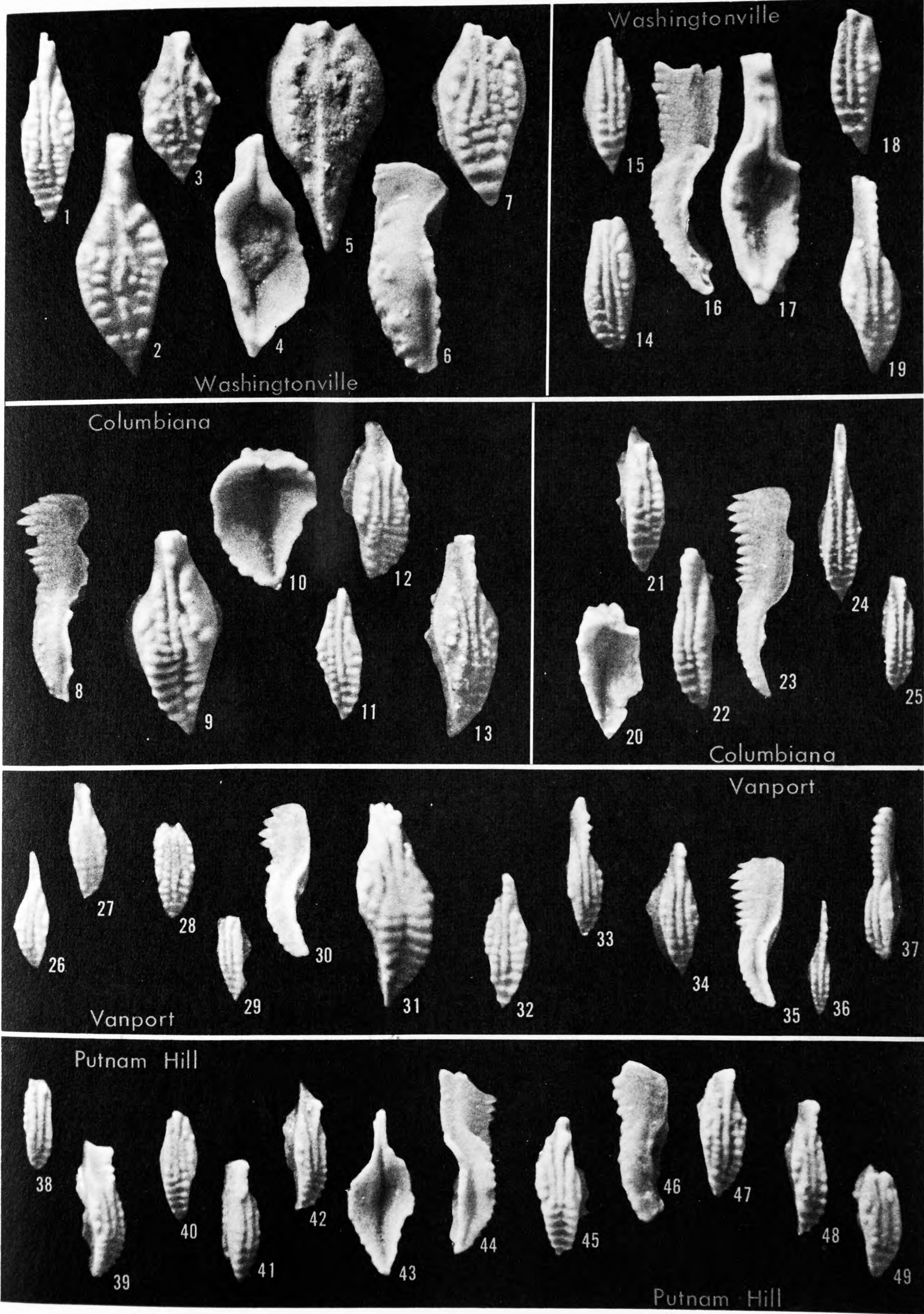
STREPTOGNATHODUS

all figures $\times 40$

Figures 1-13--*Streptognathodus cancellosus*, figures 1-7 from Washingtonville Member, 1-3,5,7 oral views, localities 8,9,9,26, and 9, respectively; 4 aboral view, locality 9; 6 outer lateral view, locality 26; figures 8-13 from Columbiana Member, 8 lateral view, locality 20; 9, 11-13 oral views, localities 20,4,4, and 1, respectively; 10 aboral view, locality 20.

Figures 14-25--*Streptognathodus oppletus*, figures 14-29 from Washingtonville Member, 14,15-18,19 oral views, localities 23,17,22,13,13, and 13, respectively; 16 lateral view, locality 22; 17 aboral view, locality 13; figures 20-25 from Columbiana Member, 20 aboral view, locality 5; 21, 22,24,25 oral views, localities 5,5,21, and 21, respectively; 23 lateral view, locality 21.

Figures 26-49--*Streptognathodus* spp., figures 26-37 from Vanport Member, 26-29, 31-34,36,37 oral views, localities 4,4,4,7,35,36,24,15,15, and 15, respectively; figures 30,35 lateral views, localities 3 and 15, respectively; figures 38-49 from Putnam Hill Member, 38-42,45,47-49 oral views, localities 4,1,4,1,1,2,22,11, and 11, respectively; 43 aboral view, locality 2; 44,46 lateral views, localities 2 and 22, respectively.



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A P P E N D I X A

TECHNIQUES

Collecting procedures.—All localities sampled in this study are listed in APPENDIX B. With few exceptions, the stratigraphic sections chosen for sampling were those which had been measured by Ferm and his students. Some others were selected from his files that originally had been measured by others and which he, in turn, had extracted from the literature. A very few localities were selected from other publications, notably the conodont localities of Sturgeon and Youngquist (1949). An effort was made by consulting Ferm, Flores, Roberts, and Zimmerman to obtain localities which would give adequate coverage not only geographically and stratigraphically, but also to obtain characteristic samples for each unit as well as departures from the norm. The result of this preparation was the selection of approximately 80 localities distributed more or less evenly from western Pennsylvania, across the entire Ohio outcrop, to northeastern Kentucky.

Most collections were made during the summer of 1965. Some additional localities were subsequently added and previous ones recollected during the summer of 1966. In addition to my collecting, and generally prior to the first field season, some samples were given to me by Ferm, Flores, Pedersen, Roberts, and Zimmerman.

Because most Allegheny units are less than three feet thick, it was usually possible and practical to sample an entire lithosome as a single sample or subsample. On occasion it was necessary to take several subsamples within a single lithosome, bounded by arbitrary footages rather than lithosome boundaries. Generally, the

amount of material taken for each sample or sample was between 1 and 3 kilograms. The Allegheny material collected and processed in this manner included several hundred individual samples and subsamples with an aggregate weight of well over a half a metric ton.

Laboratory procedures.-All samples were dried, weighed, and subjected to a variety of treatments depending upon their rock type. The calcareous rocks were digested in dilute acetic acid (ca. 10%) until all carbonate material was dissolved. This treatment is slow, but effective, and adequate for normal limestones and dolomites. Siderites, in comparison, are virtually insoluble in this acid, and essentially resisted treatment, as did cherts. Both of these rock types were treated with hydrofluoric acid on an experimental basis, but the cost compared with the acid consumption and the results achieved did not justify its continuation. Cherts and siderites are common rock types in the Allegheny and both contain conodonts, making it unfortunate that no effective and economical means to extract them could be devised.

Argillaceous rocks were treated with Varsol, a petroleum-derivative solvent, and washed with water. The results of this treatment were variable. Washed residues commonly contained large amounts of calcareous matter (shell debris, etc.), so they were subsequently acidized also.

Based on a variety of factors, the residues from either treatment ranged from extremely small amounts to ones which in weight and volume were only slightly smaller than the original rock before treatment. Routinely, nearly all samples were separated magnetically with a Franz Isodynamic Separator. The resulting concentrate

consisted almost entirely of quartz in its various forms, pyrite, and phosphate (including conodonts). Further concentration, where necessary, was accomplished by heavy liquids (bromoform, sp. gr. = 2.9) which separated the pyrite and phosphate from the lighter quartz. A final separation for samples rich in pyrite, was to float the phosphate and sink the pyrite in a second heavy liquid (methylene iodide, sp. gr. = 3.2), yielding a concentrate almost entirely of phosphate. From the concentrates, at whatever stage they were sufficiently reduced, all of the specimens were picked under the binocular microscope and arranged taxonomically on glued cardboard slides. Counts were made of each taxon and the total frequency of conodonts per kilogram was calculated for each sample or subsample.

Photographic techniques.-Selection for plates was probably more random than for most paleontologic works. Although not truly "random" samples of the fauna, the specimens were selected more on the bases of reasonable completeness of essential parts and ability to photograph well than on any preconceived notion of what a particular taxon should look like. This is especially true of the four plates illustrating specimens assigned to *Idiognathodus delicatus*. No precisely random sample is possible, nor necessarily is desirable, with such subjects, but because of a relatively large number of individual figures, there emerges a reasonably accurate portrayal of the material actually encountered.

The selected specimens were mounted on individual slides, whitened with magnesium oxide, and photographed with a 35 mm. camera equipped with bellows and a photographic objective. Lighting was provided by one microscope lamp (fill-in), and one Tensor lamp

(hi-light). Image enlargement on the negative was approximately $\times 12$, with a subsequent increase to $\times 80$ being made through the enlarger during printing, prior to the final photographic reduction to $\times 40$ for the half tones.

A P P E N D I X B

REGISTER OF COLLECTING LOCALITIES

Localities, as distinct from samples, have been numbered in two different ways in my data. One is Ferm's system and consists of the name or abbreviation of the 15' quadrangle on which the locality is located, followed by a serial (acquisition) number for that particular locality. Therefore each quadrangle has a series of numbered localities from 1 to n with no particular geographic or stratigraphic arrangement within the boundaries of the quadrangle. A system of this sort is not readily adaptable for the computer. To provide a uniform, entirely numerical location system, and also to precisely locate the localities, the geographic coordinates of each were determined to one second of longitude and latitude. Although these can be handled directly by the machine, their size (14 digits) makes them unsuitable for routine card sorting, and each set of coordinates was assigned an arbitrary serial number. This provided a second number, which was equivalent to one of Ferm's, and which was used in the organization of this register.

Samples were numbered by still a third set of numbers, serially within each stratigraphic unit. As such, they constitute acquisition numbers also, similar to Ferm's system, but organized by stratigraphic unit rather than location (quadrangle). Designations for the samples and subsamples consist of three basic elements. The middle part of each sample designation consists of three or four letters representing the stratigraphic unit: PHLS = Putnam Hill Member, either limestone or shale, VLS = Vanport Member, CHLS =

Columbiana (Hamden) Member, WSH = Washingtonville Member (either shale or limestone in the few places where it occurs). A number appears before these abbreviations and represents the serial number of the particular sample from that stratigraphic unit. Therefore these are not directly related to the locality itself, and different units at the same locality will normally bear different serial number prefixes. Finally, serial letter suffixes may follow the abbreviation of the stratigraphic unit. These sequentially lettered suffixes represent subsamples taken within a unit at a locality. Nothing is used to designate whether these subsamples represent parts of the unit taken at different stratigraphic positions, as lateral equivalents, or even as representatives of precisely equivalent strata merely collected at different times. All are considered simply as subsamples, although records detailing their natures are maintained. The figures illustrating the sample distribution (pls. 10-13) include examples of their use. Examples of the sample/subsample designations of this system include: 31PHLS = the thirty-first sample of the Putnam Hill Member, or the thirty-first Putnam Hill *locality*, and the entire unit was sampled a single time as an entity in a single sample; 20CHLSB = the second subsample from Columbiana locality 20.

This system gives numbers to units at localities rather than the localities themselves and permits different units at the same locality to have different numbers. These numbers are the ones employed on the maps (pls. 10-13) and are also used for discussions in the text. These sample numbers are arrayed under the proper unit for each locality number. A few of these numbers are followed by a question mark indicating that some doubt exists as to whether or not

the sample actually came from that unit. Several possible explanations of how these came into being can be given, although they are few in number, and for the most part could not contribute any significant deviation from any of my conclusions. They rarely indicate possible miscorrelation between units.

A few comparative Pottsville and Midcontinent localities are similarly listed in the following register.

A double page format is used for the register to provide maximum information for the localities, organized into columns as follows:

LEFT PAGE

1. The arbitrary locality number. These numbers were assigned to the different sets of geographic coordinates to satisfy computer requirements for a single short number to represent a long series of numbers.

2. My sample numbers for the Putnam Hill samples appear in this column under "PH", and align with the localities (in rows) to give the number at any particular locality.

3. Under "VPT" the same information for the Vanport as for the Putnam Hill in 2, above.

4. Under "COL" are the Columbiana sample numbers.

5. Under "WSH" are the Washingtonville sample numbers.

6. Under "DR" is the single productive Dorr Run locality.

7. This column contains north latitude to one second.

8. This column contains west longitude to one second.

9. The name of the 15' quadrangle where the locality is situated.

10. Ferm's locality number, which along with the quadrangle name, forms his complete locality designation and which is represented by the arbitrary locality number in the first column.

RIGHT PAGE

1. The arbitrary locality number is repeated to index the page.
2. The quarter of the quarter section, or the half of the quarter section as appropriate.
3. The quarter section or half section as appropriate.
4. The section number.
5. The township, employing the common Ohio practice of listing the political name of the township rather than the township and range designation.
6. The county.
7. The state if other than Ohio.
8. References to the author and page where the measured section has been published. F = Flores, R = Roberts, W = Webb, Z = Zimmerman, GSO = Ohio Geological Survey file number, GSO B = Ohio Geological Survey Bulletin number, followed by page number; finally those sections that do not list such a source are not known to have been published and can be found in Ferm's files.

loc. no.	PH	VPT	COL	WSH	DR	N. latt.			W. long.			15' quad.	Ferm's loc.
1		1				40	40	54 80	20	30	Beaver		2
2	1					39	38	19 82	13	19	N. Lexington		18
3	2					40	23	55 81	33	20	N. Comerstown		14
4	3	3	6?			40	29	16 81	28	35	Uhrichsville		14
5	4	28	3?	8		40	12	33 81	56	37	Conesville		18
6	5					39	48	05 82	14	28	N. Lexington		25
7	6		9?			40	40	20 81	24	07	Dover		59
8				1		39	59	21 81	56	21	Philo		11
9				2?		39	57	02 82	10	17	Zanesville		30
10		4				39	14	29 82	27	36	Wilkesville		41
11	10	5				40	56	09 81	22	26	Canton		8
12	25					40	39	54 81	21	44	Dover		19
13		7				40	43	59 80	20	24	Beaver		7
14		8	23?	24		40	53	10 80	15	08	New Castle		2
15	28	9				40	57	27 81	04	19	Alliance		15
16	7					40	36	40 81	30	22	Navarre		24
17	8?					40	42	47 80	17	43	Beaver		12
18	9					40	26	43 81	41	27	N. Comerstown		2a
19	11					39	38	22 82	13	22	N. Lexington		17
20	12					39	56	15 82	00	51	Zanesville		31
21	13					39	27	30 82	16	43	Zaleski		70
22	1Z	11				not calculated					Wilkesville		53
23	2Z					not calculated					Wilkesville		42
24		12				38	38	18 82	41	23	Ironton		40
25		13				38	37	37 82	39	31	Ironton		41a

loc. no.	$\frac{1}{4}(\frac{1}{2})$	$\frac{1}{4}(\frac{1}{2})$	sec.	township	county	state if not Ohio	reference-remarks
1	-	-	-	Borough	Beaver	Penna.	Vanport type
2	-	NE	5	Salt Lick	Perry		R44
3	NW	SW	12	Jefferson	Tuscarawas		Z106
4				Goshen	Tuscarawas		Z102,103
5	SW	SE	8	Virginia	Coshocton		Z118,119
6	NW	NE	7	Pike	Perry		R44,45
7	SE	SW	20	Pike	Stark		Z90
8	NE	SE	9	Washington	Muskingum		F107
9	SW	SE	24	Hopewell	Muskingum		F131,132
10	NE	NW	27	Elk	Vinton		W65
11	SE	SW	21	Lake	Stark		Z82
12	NE	NE	27	Pike	Stark		GS0 15065
13	-	-	-	Brighton	Beaver	Penna.	R43,44
14	-	-	-	Big Beaver	Lawrence	Penna.	Wampum Quarry
15	NE	NE	18	Smith	Mahoning		Z74
16	N	NW	16	Lawrence	Tuscarawas		Z94
17	-	-	-	Rochester	Beaver	Penna.	R45
18	NE	SW	25	German	Holmes		Z107
19	SW	SE	5	Salt Lick	Perry		F98,99
20	SE	NE	1	Springfield	Muskingum		F132
21	SW	SW	36	York	Athens		F118
22	N	SW	12	Milton	Jackson		W74
23	NW	SW	32	Madison	Vinton		W66,67
24	-	SW	17	Elizabeth	Lawrence		W100
25	-	NE	21	Elizabeth	Lawrence		W101

loc. no.	PH	VPT	COL	WSH	DR	N. latt.			W. long.			15' quad.	Ferm's loc.
26		14				38	31	08 82	49	16		Ironton	36
27		15				38	29	01 82	39	52		Ashland (7½)	19
28					3	40	41	40 80	18	02		Beaver	8
29			1			40	38	52 80	30	01		Wellsville	32
30				4	1	40	37	11 80	39	02		Wellsville	42
31		16				38	22	18 82	45	56		Rush (7½)	16
32		17	Omit										
33		18				not calculated						Oak Hill	44
34		19				38	50	16 82	37	57		Oak Hill	35
35		20				38	53	49 82	36	06		Oak Hill	34
36	3Z	21				not calculated						Wilkesville	44
37	14	22				39	14	46 82	27	21		Wilkesville	40
38	15	23				39	14	46 82	30	32		Jackson	24
39	4Z	24				39	16	17 82	27	04		Zaleski	61
40	16					not calculated						Zaleski	87
41	17					not calculated						Zaleski	23
42	18					not calculated						Zaleski	44
43					2	39	26	44 82	20	18		Zaleski	67
44		25				not calculated						Logan	17
45		26				not calculated						Logan	19
46				5		not figured						Zanesville	25
47		27	2	6		39	48	48 82	12	50		Zanesville	24
48					3	not calculated						Philo	12a
49				7		not calculated						Philo	12b
50	19	29				40	13	03 81	56	48		Conesville	17

loc. no.	$\frac{1}{4}$ ($\frac{1}{2}$)	$\frac{1}{4}$ ($\frac{1}{2}$)	sec.	township	county	state if not Ohio	reference-remarks
26	NW	SE	26	Upper	Lawrence		W97
27	-	-	-	-	Boyd	Kentucky	W121
28	-	-	-	Moon	Beaver	Penna.	Monaca cut
29	-	-	-	Ohio	Beaver	Penna.	Smith's Ferry
30	E	NE	11	Yellow Creek	Columbiana		Rte. 45 Wellsville
31	-	-	-	-	Boyd	Kentucky	W140
32	Omit						
33	SE	SE	35	Jefferson	Jackson		W92
34	NE	SE	4	Washington	Lawrence		W88
35	SW	NW	14	Jefferson	Jackson		W87,88
36	NW	NW	22	Milton	Jackson		W68
37	-	SE	22	Elk	Vinton		W64
38	SW	SW	20	Elk	Vinton		W80,81
39	NE	NE	14	Elk	Vinton		F113,114
40	SE	SE	3	Elk	Vinton		F124,125
41	SE	SE	32	Brown	Vinton		GSO B31,176
42	NE	NE	27	Starr	Hocking		GSO 9320
43	NW	NW	16	Starr	Hocking		F117
44	NW	SW	25	Jackson	Perry		GSO B48,119
45	NW	SW	31	Pike	Perry		GSO B48,203
46	SW	SW	10	Clayton	Perry		F128,129
47	NE	SE	5	Clayton	Perry		F128
48	SW	NE	23	Washington	Muskingum		F107,108
49	SE	NE	24	Washington	Muskingum		F107,108
50	-	NW	8	Virginia	Coshocton		Z117,118

loc. no.	PH	VPT	COL	WSH	DR	N. latt.			W. long.			15' quad.	Ferm's loc.
51		30		9		40	13	11 81	57	34		Conesville	15
52				10		40	15	45 81	53	24		Coshocton	20
53				11		not calculated						N. Comerstown	23
54	20		4	12		40	19	59 81	31	49		N. Comerstown	24
55			5			40	23	20 81	28	15		Uhrichsville	15
56	21					40	33	33 81	24	54		Dover	1
57	22	31	7			40	30	03 81	31	36		Navarre	29
58			8	13		40	31	53 81	32	22		Navarre	30
59	23					40	37	47 81	36	41		Navarre	34
60	24	32				40	40	13 81	25	50		Dover	16
61	Omit												
62	26					40	39	43 81	22	24		Dover	58
63	Omit												
64					4	not calculated						Dover	68
65	27					40	53	47 81	16	56		Canton	2
66			10	14		40	47	26 81	08	58		Alliance	27
67		33				not calculated						Alliance	21
68			11			41	56	59 81	00	34		Alliance	-
69			12			40	52	42 80	59	30		Lisbon	-
70			13			40	56	32 80	50	28		Lisbon	-
71			14			not calculated						Lisbon	-
72			15			not calculated						Lisbon	-
73				15		not calculated						Lisbon	6
74				16		not calculated						Columbiana	29
75					5	not calculated						Wellsville	15

loc. no.	$\frac{1}{4}(\frac{1}{2})$	$\frac{1}{4}(\frac{1}{2})$	sec.	township	county	state if not Ohio	reference-remarks
51	NE	SW	3	Virginia	Coshocton		Z116
52	-	-	-	Jackson	Coshocton		Z111,112
53	-	-	-	White Eyes	Coshocton		Z107,108
54	SW	E	11	Salem	Tuscarawas		Z108
55	-	-	-	Warwick	Tuscarawas		Z103,104
56	NW	SW	6	Fairfield	Tuscarawas		GSO 11346
57	NE	SE	1	Dover	Tuscarawas		Z96,97
58	NE	SE	19	Dover	Tuscarawas		Z97,98
59	-	-	-	Wayne	Tuscarawas		GSO 14251
60	NE	NE	25	Bethlehem	Stark		GSO 13504
61	SW	NE	7	Pike	Stark		Z91,92
62	S	NW	27	Pike	Stark		Z89,90
63	SE	NW	17	Sandy	Stark		GSO 14660
64	SW	NE	33	Osnaburg	Stark		Z91
65	SW	SW	32	Marlboro	Stark		Z81
66	NW	SE	9	Paris	Stark		Z79,80
67	SE	NE	19	Smith	Mahoning		Z77
68	NW	SW	14	Smith	Mahoning		mine dump
69	W	C	12	Knox	Columbiana		S&Y 382
70	NE	NE	19	Green	Mahoning		GSO 3770
71	-	NW	21	Green	Mahoning		GSO 3772
72	SE	SE	15	Salem	Columbiana		mine dump
73	NE	NW	23	Center	Columbiana		Lisbon bridge
74	-	NE	20	Elk Run	Columbiana		along road
75	SE	NE	14	Madison	Columbiana		along U.S. 30

loc. no.	PH	VPT	COL	WSH	DR	N. latt.			W. long.			15' quad.	Ferm's loc.
76			16	17	6?	40	40	47 80	31	28	Wellsville	86	
77		34	17			40	47	12 80	31	53	Columbiana	12	
78			18			not calculated					Columbiana	14	
79			19	18		40	56	23 80	32	36	Columbiana	13	
80			20			40	58	47 80	38	36	Columbiana	17	
81			21			40	58	53 80	35	17	Columbiana	16	
82		35				40	59	45 80	31	20	Columbiana	15	
83		36				41	02	18 80	33	03	Youngstown	9	
84				19		40	33	47 80	39	58	Wellsville	52	
85				20		40	35	08 80	40	10	Wellsville	72	
86		37				40	37	34 80	36	44	Wellsville	36	
87				22	7?	40	39	34 80	35	21	Wellsville	45	
88			22			40	37	40 80	25	56	Beaver	11	
89		38				40	40	00 80	21	57	Beaver	20	
90				23		40	45	04 80	20	20	New Castle	7	
91				25	8	40	50	15 80	22	42	New Castle	6	
92			24	26	9?	40	49	15 80	25	25	New Castle	8	
93	Omit												
94	31	+ 10 Lower Mercer				39	58	00 82	17	02	Thornville	-	
95		39				not calculated					Lisbon	1	
- Anna Member, Pawnee Formation						not calculated					Lexington West (7½)		
- 2 Lower Mercer						not calculated					Zanesville	-	
- 4 Lower Mercer						41	02	20 80	33	03	Youngstown	8	
- 6 Upper & 9 Lower Mercer						not calculated					Zanesville	-	
- 8 Upper Mercer						40	03	34 81	58	08	Conesville	-	
-Early Pennsylvanian shale						not calculated					unkown	-	

loc. no.	$\frac{1}{4}(\frac{1}{2})$	$\frac{1}{4}(\frac{1}{2})$	sec.	township	county	state if not Ohio	reference-remarks
76	-	C	24	St. Clair	Columbiana		Grimm's Bridge
77	SW	SW	12	Middleton	Columbiana		Negley complex
78	NE	SW	23	Springfield	Mahoning		Petersburg strip
79	-	NE	23	Springfield	Mahoning		Subrosa School
80	NE	SW	1	Beaver	Mahoning		Coalmines strip
81	SE	NW	4	Springfield	Mahoning		New Middleton
82	-	-	-	Poland	Mahoning		Bessemer Quarry
83	-	-	-	Poland	Mahoning		Lowellville pit
84	SE	NW	7	Saline	Jefferson		along Yellow Creek
85	SW	SW	9	Yellow Creek	Columbiana		opp. Baker Island
86	SW	SW	30	Liverpool	Columbiana		East Liverpool
87	NE	NW	24	Liverpool	Columbiana		California Hollow
88	-	-	-	Industry	Beaver	Penna.	Cook's Ferry
89	-	-	-	Industry	Beaver	Penna.	creek at Merrill
90	-	-	-	Patterson	Beaver	Penna.	Patterson triangle
91	-	-	-	Big Beaver	Beaver	Penna.	New Galilee strip
92	-	-	-	Darlington	Beaver	Penna.	Darlington strip
93	Omit						
94	SE	SW	30	Hopewell	Muskingum		Fairview School
95	NE	NW	4	Green	Mahoning		GSO 15068
-	NE	NW	33	T51N,R27W	Lafayette	Mo.	Gunnell, 1931
-	S	NE	18	Hopewell	Muskingum		Poverty Run
-	-	-	-	Poland	Mahoning		Grindstone Run
-	C	NE	20	Newton	Muskingum		along creek
-	-	-	-	Madison	Muskingum		along Ohio 666
-	-	NW	1	T75N,R20W	Marion	Iowa	Youngquist & Downs

APPENDIX C

STATISTICAL DATA, TESTS, AND RESULTS

Procedure.—The specimen counts from each productive sample, along with the programs and the explanation of the data entries are completely listed on the tape (original) or printouts (all other copies) located in the pocket at the end of this dissertation (as APPENDIX D). The tape is "stacked" in the following manner:

"BLK=10 DCN. 556 BPI".

Through its use , it is possible to reproduce all the punch cards for both programs and data.

Specimen counts.—From the data on tape or printouts in the pocket, the number of specimens/taxon/subsample/sample/stratigraphic unit can be determined. Total specimen counts of the 21 categories included all specimens for each unit and break down as follows:

Taxon	Unit				
	WSH	COL	VLS	PH	Total
1. <i>Cavusgnathus</i> spp.	158	312	3,099	213	3,782
2. <i>Gnathodus</i> spp.	20	322	1,087	196	1,625
3. <i>Idiognathodus</i> spp.	2,741	10,899	4,279	2,708	20,627
4. <i>Streptognathodus</i> spp.	1,481	1,210	305	141	3,137
5. <i>Ozarkodina</i> spp.	233	559	548	518	1,858
6. <i>Spathognathodus</i> spp.	171	501	1,511	362	2,545
7. <i>Hibbardella subacoda</i>	1	15	41	86	143
8. <i>H.</i> n.spp. 1&3	3	5	89	13	110
9. <i>H.</i> n.sp. 2	7	20	81	7	115

Taxon	Unit				
	WSH	COL	VLS	PH	Total
10. <i>Hindeodus</i> spp.	14	63	327	95	499
11. <i>Ligonodina</i> except 4&10	102	60	192	411	665
12. <i>L.</i> n.sp. 4	49	196	536	110	891
13. <i>L.</i> n.sp. 10	0	0	68	0	68
14. <i>Lonchodina</i> spp.	0	40	137	143	320
15. <i>Metalonchodina</i> spp.	0	3	22	52	77
16. <i>Neoprioniodus</i> except 7&10	5	13	38	87	143
17. <i>N.</i> n.sp. 7	0	0	10	7	17
18. <i>N.</i> n.sp. 10	0	5	46	4	55
19. New genus A, n.sp. 3	32	145	273	67	517
20. New genus B, n.sp. 1	57	162	366	77	662
21. Others	373	1,175	4,438	2,666	8,652
TOTALS	5,347	15,705	17,193	7,963	46,508

Recombining these taxa into the four groups of associated taxa results in the following counts:

Group	Unit				
	WSH	COL	VLS	PH	Total
<i>Cavusgnathus</i> -biofacies	161	322	3,302	240	4,025
Ubiquitous forms	5,019	14,666	11,168	6,591	39,434
Appalachian forms	199	586	1,593	363	1,701
Midcontinent forms	8	131	430	779	1,348
TOTALS	5,347	15,705	11,193	7,973	46,508

Because the diversity *within* the Vanport Member is greater than that between some members, at least as far as these categories are concerned, it is worthwhile to subdivide the Vanport into southern limestone, southern shale, northwestern limestone, northeastern limestone, and northern shale.

"Shale" here includes associated thin-bedded limestones. These are rather homogeneous groupings except the northern shale which includes shales and thin limestones associated with both the northwestern and northeastern limestones. Divided among the 21 categories the faunal counts look like this:

Taxon	Subdivision					
	S.LS.	S.SH.	NW LS.	NE LS.	N.SH.	Total
1. <i>Cavusgnathus</i> spp.	104	2,915	44	0	36	3,099
2. <i>Gnathodus</i> spp.	194	585	21	220	67	1,087
3. <i>Idiognathodus</i> spp.	535	1,504	158	915	1,167	4,279
4. <i>Streptognathodus</i> spp.	117	164	13	5	6	305
5. <i>Ozarkodina</i> spp.	42	873	12	182	139	1,248
6. <i>Spathognathodus</i> spp.	126	937	16	315	117	1,511
7. <i>Hibbardella subacoda</i>	1	2	1	12	25	41
8. <i>H.</i> n.spp. 1&3	5	80	2	1	1	89
9. <i>H.</i> n.sp. 2	13	56	1	11	0	81
10. <i>Hindeodus</i> spp.	45	200	4	50	28	327
11. <i>Ligonodina</i> except 4&10	6	12	10	61	103	192
12. <i>L.</i> n.sp. 4	70	318	2	92	54	536
13. <i>L.</i> n.sp. 10	4	63	0	1	0	68
14. <i>Lonchodina</i> spp.	6	7	1	54	69	137

Taxon	Subdivision					
	S.LS.	S.SH.	NW LS.	NE LS.	N.SH.	Total
15. <i>Metalonchodina</i> spp.	0	1	2	9	10	22
16. <i>Neoprioniodus</i> except 7&10	1	0	0	13	24	38
17. <i>N.</i> n.sp.7	0	0	0	10	0	10
18. <i>N.</i> n.sp.10	3	43	0	0	0	46
19. New genus A, n.sp. 3	29	158	4	52	30	273
20. New genus B, n.sp. 1	42	253	4	46	21	366
21. Others	308	1,677	55	1,281	117	3,438
TOTALS	1,651	9,848	350	3,330	2,014	17,193

Regrouping the 21 categories into the four groups of taxa produces the following widely divergent counts:

Group	Subdivision					
	S.LS.	S.SH.	NW LS.	NE LS.	N.SH.	Total
<i>Cavusgnathus</i> -biofacies	116	3,101	46	1	37	3,302
Ubiquitous forms	1,322	5,740	275	2,918	1,613	12,866
Appalachian forms	199	985	15	262	133	1,594
Midcontinent forms	14	22	14	149	231	430
TOTALS	1,651	9,848	350	3,330	2,014	17,193

Purpose of tests.-From the standpoint of the paleontologist, the purpose behind the statistical tests was to evaluate the taxonomic differences between samples in space, not in time, as no tests were directly related to biometrics and phylogeny. Therefore, the conclusions derived from these tests were intended to explain the various ways that taxa can occur together, and from observations and previous

knowledge, to appraise the biologic, ecologic, and geologic implications of these conclusions. It was hoped also that these tests would provide new information, not apparent from observation, about the ways in which these faunas can differ.

From the standpoint of a statistician, tests such as these simply compared the categories in two or more columns to see if they contained enough observations to test, and if so, to see if they differed more from each other than could be expected by chance.

Technique of testing.—The basic testing procedure utilized was the χ^2 (chi-square) distribution. Each of the 21 taxonomic categories constituted a row, and the samples or subsamples to be tested formed the columns. Two columns and up to 21 rows could therefore give up to 42 cells for the maximum information from the simplest possible comparison (between two samples). The basic computer program gave either row and column designation, the expected values for these designations if less than 5.0, and the total χ^2 value and degrees of freedom for the entire matrix. By the substitution of one instruction card for another, the program would cause the listing of all observed and expected values for each cell, regardless of value, in order, but without designating the row and column numbers. It also gave the total χ^2 value and degrees of freedom for the matrix as before. All tests were first run in the former way to test for low expected values so that they might be eliminated (less than 1.0 for these tests), and then rerun with the altered instructions to obtain more complete information. Most tests included only a very few of the 21 possible rows. Neither method of operation gave the χ^2 values for the individual cells, although all

data to calculate them were printed. Thus, the machine calculated the expected value for each cell by multiplying its observed row and column totals, then dividing by the grand total value for the matrix. It continued by solving the equation:

$$\chi^2 = \frac{(\text{observed} - \text{expected})^2}{\bar{\text{expected}}}$$

to determine the value for each cell. Next the cell values were added together to produce the total χ^2 value for the matrix. Finally, the machine calculated the degrees of freedom:

$$\text{degrees of freedom } (df) = (\text{rows} - 1)(\text{columns} - 1)$$

and printed out this information.

In addition to several dozen tests with the large computer, a few dozen simple tests, requiring more time to compare and prepare the deck of punch cards than to calculate, were run with the aid of an Olivetti-Underwood Programma 101 desk computer.

At an early stage it became apparent that many tests were statistically significant which showed no predictable or even consistent biologic differences. It became axiomatic that, the larger the number of individuals used in a test, the greater the χ^2 value would exceed the tabular value for that number of degrees of freedom. Stated differently, larger samples generally had χ^2 values which increased too fast for their degrees of freedom. This difficulty was partially eliminated by comparing the resulting χ^2 values from different tests, each weighted according to its df , against one another. This was accomplished by treating the χ^2 values according to

the F distribution:

$$F = \frac{\frac{\chi^2_1}{df_1} \text{ (larger)}}{\frac{\chi^2_2}{df_2} \text{ (smaller)}}$$

The benefit of this testing was that it sorted out those tests that had really large deviations from the expected distribution. As an example, the northeastern Vanport Limestone at locality 36 was sampled in 22 subsamples. A matrix comparing all 22 of these subsamples generated a χ^2 of nearly 500. Although the number of degrees of freedom was also large (105), the tabular χ^2 for this matrix was only about 125. No two individual subsamples at this locality show significance, no trends within the fauna can be observed from subsample to subsample, in fact, this locality contains about the most internally homogeneous faunas seen anywhere in the Allegheny. Along with everything else, the numbers of specimens in these subsamples were large. Despite the huge disparity in actual and tabular χ^2 values, the resulting number for an F test is 500 divided by 105 or approximately 5.0. This figure compared with others, did indeed establish less variation here than at most other places confirming the subjective evaluation.

Another bothersome side effect of these tests involved comparison of a very large sample with a very small one. No matter how different might be their compositions, the numerical weight of the larger tended to overcome the readily apparent differences. If

the one is small enough, there is some doubt about the validity of the test, of course, but the test can be misleading before that stage is reached. Some of this disparity in size could be eliminated by legitimate regroupings, but it was commonly necessary to divide each category in the larger sample by some constant to bring it near the parity with the corresponding category in the smaller sample. Although this procedure is dubious at best, failure to do so obscures differences apparent on even casual observation.

Testing sequence.-Several types of tests were employed in a progressive sequence. Some others were later made, especially the *F* tests, for some, but not all, the results. The basic types were:

Type I.-Simply stated, the Type I tests compared subsamples within a single lithosome, within a single unit, within a locality. At this level, all limestones were considered the same lithosome as were all shales, regardless of fauna, lithology, or stratigraphic position within the unit.

Type II.-These were between the basic lithosomes of the Type I tests (most commonly between limestone and shale), still within a single stratigraphic unit, at a single locality.

Type III.-Type III tests were designed to regroup the lithosomes of the Types I and II tests into other possible, and reasonable, combinations. These were based on physical attributes such as color (placing a dark, thin-bedded limestone with the associated dark, calcareous shale rather than the laterally equivalent light colored, massive limestone at Vanport locality 24, for example), and stratigraphic position. Several examples of vertical differences dictated the latter groupings, as for example, in a shale-limestone-shale

succession where the fauna of the limestone and either the over- or underlying shale are similar to each other, and different from the other shale (as at Vanport loc. 7).

Type IV.-These tests united similar lithosomes from related localities within a stratigraphic unit within a basin. For example, all Putnam Hill Limestones were compared with each other, and all Columbiana Shales were compared with each other.

Type V.-Basin-wide comparisons between lithosomes constituted the Type V tests. The total Putnam Hill Shales were now compared with the total Putnam Hill Limestones. Vanport sub- and superbasin lithologies were similarly tested.

Type VI.-The Type VI tests were comparisons between stratigraphic units. Results of these tests were too generalized to be of much value. On this scale it is evident that:

- 1) *Cavusgnathus* is most abundant in the Vanport.
- 2) *Gnathodus* also is most abundant in the Vanport and decreases sharply thereafter.
- 3) *Idiognathodus* and *Streptognathodus* gain or lose at the other's expense, *Streptognathodus* increases in successively younger units.
- 4) No distribution pattern of significance can be attached to the occurrences of *Ozarkodina*, *Spathognathodus*, and the "others" category.
- 5) *Hibbardella subacoda* decreases in each unit from the Putnam Hill upward. The same is true, at least in relative abundance, for the other Midcontinent taxa, *Ligonodina lexingtonensis*, *L. typa*,

Lonchodina spp., *Metalonchodina* spp., and *Neoprioniodus* except n.spp. 7 & 10.

6) *Hibbardella* n.spp. 1 & 3, *Ligonodina* n.sp. 10, and *Neoprioniodus* n.sp. 10, the associates of *Cavusgnathus*, have distributions parallel to and coincident with that of *Cavusgnathus*.

7) Appalachian taxa, *Hibbardella* n.sp. 2, *Hindeodus* spp., *Ligonodina* n.sp. 4, *Neoprioniodus* n.sp. 7, and new genera and species A-3, and B-1 are most abundant in the Vanport, more abundantly represented in the Columbiana than in the Putnam Hill, and least abundant in the Washingtonville, although proportionally more abundant in that unit than in any other Allegheny unit.

8) Stated differently, non-platforms are most abundant in those units having the most limestone samples. Therefore the Vanport has the most, the Putnam Hill next, followed by the Columbiana, and the Washingtonville the least. The preservation/recovery influence is undeniable. However, there is presently no platform evidence that there was selective elimination. Indeed the Appalachian taxa are generally more fragile than their Midcontinent counterparts, yet they are the forms most common in the Washingtonville which shows the greatest apparent loss of non-platform conodonts.

Results of χ^2 tests.—The results of the tests will be listed in the format of flow charts. Each type test will be listed above the group of tests, and the tests of that type will be arrayed below it. Symbols used for each test are:

location number (parenthetical attention to footnote at end
size of matrix as rows \times columns of section)
calculated χ^2 (tabular χ^2 , .05 level)

The tabular χ^2 value has the symbol "+" following the parenthesis if the difference from the calculated χ^2 is significant. Some which exceed the tabular value by a small amount are not so listed.

PUTNAM HILL TESTS

I-Putnam Hill Limestones:

12	4	6	24	27 ⁽¹⁾
3×2	9×2	4×2	5×2	2×4
6.9(5.9)	15.1(15.5)	4.0(7.8)	2.0(9.4)	13.5(7.8)+

I-Putnam Hill Shales:

4	2	22 ⁽²⁾	24	28
5×2	8×2	7×3	2×2	2×2
3.2(9.5)	15.9(14.1)	38.7(21.0)+	0.1(3.8)	0.1(13.8)

II-Putnam Hill Limestones vs. Shales:

11	12 ⁽³⁾	4 ⁽⁴⁾	20 ⁽⁵⁾
5×2	3×2	16×2	11×2
10.9(9.5)	19.3(5.9)+	196.2(24.9)+	60.1(18.3)+

2 ⁽⁶⁾	3 ⁽⁷⁾	22 ⁽⁸⁾	23
11×2	16×2	16×2	12×2
35.7(19.7)+	85.3(25.0)+	65.3(24.9)+	12.6(19.9)

6	24	26	10 ⁽⁹⁾	28 ⁽¹⁰⁾
7×2	6×2	8×2	12×2	7×2
7.8(12.6)	5.1(11.1)	18.6(14.0)	35.5(19.7)+	24.2(12.6)+

III-Other groupings:

3 ⁽¹¹⁾
7×4
97.8(27.9)+

IV-All Putnam Hill Limestones:

$$\begin{array}{r} \text{all}^{(12)} \\ 16 \times 5 \\ 343.6(79.1)+ \end{array}$$

IV-All Putnam Hill Shales:

$$\begin{array}{r} \text{all}^{(13)} \\ 11 \times 6 \\ 414.3(67.5)+ \end{array}$$

V-Total Putnam Hill Limestones vs. Shales:

$$\begin{array}{r} \text{all}^{(14)} \\ 20 \times 2 \\ 141.8(30.1)+ \end{array}$$

SOURCES OF DIFFERENCES

- (¹) No apparent explanation for these differences.
- (²) *Cavusgnathus* increases downward in stratigraphically arranged subsamples.
- (³) *Cavusgnathus* dominates limestone, *Idiognathodus* the overlying shale.
- (⁴) Apparently "static" in large sample.
- (⁵) Same as (⁴).
- (⁶) Same as (⁴).
- (⁷) Large variation in *Cavusgnathus* in shales overlying limestone, limestone contains virtually none.
- (⁸) Same as (⁷).
- (⁹) No apparent explanation, mostly in *Idiognathodus* vs. others.
- (¹⁰) Same as (⁹).

- (¹¹) Regrouping of 31 subsamples into top, second, third, and bottom quarters of the shale succession brought out the variations in *Cavusgnathus* more decisively and demonstrated as much or more variation in the shale as between the shale and the limestone.
- (¹²) Most of the χ^2 value for this test was derived from two localities, 4 and 23. Even then, there seems to be no distinctive pattern.
- (¹³) Four localities are mostly responsible for this large χ^2 ; 1, 11, 3, and 22. All are heavily dominated by *Cavusgnathus* in contrast to the other localities.
- (¹⁴) The source of such an involved χ^2 is difficult to pinpoint. A large part of it is "static", but it certainly shows the accumulation of lesser differences in *Cavusgnathus* vs. *Idiog-nathodus* from the different localities.

VANPORT TESTS

(SOUTHERN VANPORT)

I-Southern Vanport Limestones

15	20	23(¹)	22	24(²)
11×2	11×2	11×2	8×2	12×2
14.4(18.3)	14.3(18.3)	32.0(18.3)+	2.4(14.1)	40.1(19.7)+

I-Southern Vanport Shales:

4	24(³)
4×2	14×2
6.7(7.8)	44.7(22.4)+

II-Southern Vanport Limestones vs. Shales:

$$\begin{array}{rcl} 4 & & 22^{(4)} \\ 9 \times 2 & & 4 \times 2 \\ 14.9(15.5) & 24.9(7.8)+ & \end{array}$$

III-Other groupings:

$$\begin{array}{rcl} 24^{(5)} & & \\ 14 \times 2 & & \\ 206.4(22.4)+ & & \end{array}$$

IV-All southern Vanport Limestones:

$$\begin{array}{rcl} \text{all}^{(6)} & & \\ 6 \times 7 & & \\ 82.8(57.0)+ & & \end{array}$$

IV-All southern Vanport Shales:

$$\begin{array}{rcl} \text{all}^{(7)} & & \\ 17 \times 2 & & \\ 274.7(26.3)+ & & \end{array}$$

V-All Vanport Shales vs. all Vanport Limestones, see below.

NORTHERN VANPORT

I-Northwest Vanport Limestones I-Northeast Vanport Limestones:

$$\begin{array}{rclcl} 32 & & 35 & & 36^{(8)} \\ 2 \times 2 & & 7 \times 2 & & 6 \times 22 \\ 0.8(3.8) & & 6.4(12.6) & 478.0(124.0)+ & 8 \\ & & & & 3 \times 2 \\ & & & & 4.8(6.0) \end{array}$$

I-Northern Vanport Shales:

$$\begin{array}{rcl} 7 & & \\ 2 \times 2 & & \\ 0.05(3.8) & & \end{array}$$

II-Northern Vanport Limestones vs. Shales:

Northwestern

3
5×2
7.5(9.5)

Northeastern

7(⁹)
15×2
256.4(23.6)+

III-Other groupings:

7(¹⁰)
3×2
0.5(6.0)

IV- All northern Vanport Limestones:

Northwestern

all(¹¹)
8×2
24.1(14.1)+

Northeastern

all(¹²)
5×4
59.7(31.4)+

IV-All northern Vanport Shales:

all(¹³)
4×4
108.8(16.9)+

V-All Vanport Limestones vs. all Vanport Shales:

all(¹⁴)
16×5
4,910.3(79.1)+

SOURCES OF DIFFERENCES

(¹) No explanation for these differences.

(²) Same as (¹).

(³) Same as (¹).

(⁴) Shale dominated by *Cavusgnathus*.

- (⁵) Same as (⁴).
- (⁶) Same as (¹).
- (⁷) Differences in the degree of domination by *Cavusgnathus*.
- (⁸) Despite the huge χ^2 value, it really isn't so large when divided by its degrees of freedom: $478 \div 105 = 4.55$. Several tests were made between individual subsamples among the 22. All tests were not significantly different, regardless of stratigraphic position within the outcrop.
- (⁹) Same as (⁴).
- (¹⁰) Same as (⁴). This is combined so that the top shale and limestone (*Idiognathodus*-dominated) are compared with the bottom shale (*Cavusgnathus*-dominated). The frequency in the top two so greatly outnumbers the fauna in the lower unit that the χ^2 , although greater, is less meaningful.
- (¹¹) Same as (¹).
- (¹²) Same as (¹).
- (¹³) & (¹⁴) Genuine differences of many sorts, *Cavusgnathus* vs. *Idiognathodus*, and provincial ones, plus less certainly determinable ones make up this immense χ^2 value.

COLUMBIANA TESTS

I-Columbiana Limestones:

13 (¹)
11×2
51.5(18.3)+

I-Columbiana Shales:

$$\begin{array}{rcl} 4^{(2)} & & 21^{(3)} \\ 5 \times 2 & & 10 \times 2 \\ 61.9(15.5)+ & 37.9(16.9)+ & \end{array}$$

II-Columbiana Limestones vs. Shales:

$$\begin{array}{rcl} 4^{(4)} & & 21^{(5)} & & 20^{(6)} \\ 13 \times 2 & & 11 \times 2 & & 13 \times 2 \\ 110.7(21.0)+ & 130.9(18.3)+ & 107.8(21.0)+ & & \end{array}$$

III-Other groupings:

$$\begin{array}{rcl} 4^{(7)} \\ 10 \times 2 \\ 33.3(16.9)+ \end{array}$$

IV-All Columbiana Limestones:

$$\begin{array}{rcl} \text{all}^{(8)} \\ 9 \times 7 \\ 1,030.0(73.0)+ \end{array}$$

IV-All Columbiana Shales:

$$\begin{array}{rcl} \text{all}^{(9)} \\ 9 \times 8 \\ 2,045.9(75.0)+ \end{array}$$

V-All Columbiana Limestones vs. all Columbiana Shales:

$$\begin{array}{rcl} \text{all}^{(10)} \\ 19 \times 2 \\ 292.5(28.9)+ \end{array}$$

SOURCES OF DIFFERENCES

(¹) Probably "static" in the large sample.

(²) This locality has *Carrasgnathus*-biofacies in bottom shale and

limestone.

(³) Same as (¹).

(⁴) See (²).

(⁵) Same as (¹).

(⁶) Same as (¹).

(⁷) See (²).

(⁸) Some influence from locality 4, largely "static", however.

(⁹) Same as (⁸).

(¹⁰) Same as (⁸).

WASHINGTONVILLE TESTS

I-Washingtonville Limestones:

None

I-Washingtonville Shales:

2(¹)	8	13(²)	19
7×2	4×2	8×2	7×2
34.2(21.0)+	7.8(7.8)	122.3(14.1)+	14.7(12.6)

II-Washingtonville Limestones vs. Shales:

2
8×2
17.9(19.1)

III-Other groupings:

2(³)
6×2
31.6(11.1)+

IV-All Washingtonville Limestones:

None

IV-All Washingtonville Shales:

all (⁴)
 8×11
 772.6(91.0)+

V-All Washingtonville Limestones (1) *vs.* all Washingtonville Shales:

all (⁵)
 6×2
 247.6(11.1)+

SOURCES OF DIFFERENCES

- (¹) Bottom shale and limestone dominated by *Cavusgnathus*, top shale by *Idiognathodus*.
- (²) No definable difference.
- (³) Same as (¹).
- (⁴) The one locality, loc. 2, does not contribute that greatly to the χ^2 , most of the difference does not seem relevant.
- (⁵) The one limestone (loc. 2), is strongly dominated by *Cavusgnathus*, and contributes much to the χ^2 value.

OTHER TESTS

In addition to these standard sets of tests run for all combinations that formed at least a two by two matrix, a large number of other, similar tests were run on various parts of the fauna with either some taxa or some samples deleted. By doing this, it was possible to determine which taxa or which samples were actually contributing most heavily to the values, and the

large differences could thus be eliminated. Generally, these were the large categories and the reduction in both the number of categories and the number of individuals effected some increase in the sensitivity of the testing for those remaining. In all there were about another 25 of these tests. The F Tests were even more numerous, some 30 odd were run to compare amounts of difference.

The overall results of these F tests generally confirmed my observations about the fauna. A summary of a few of these conclusions follows:

1. The greatest homogeneity for any member is found in the Putnam Hill. This includes its entire outcrop area for all lithologies.
2. The Putnam Hill Limestone is more homogeneous than the Putnam Hill Shale.
3. Each of the massive Vanport Limestones, southern, northwestern, and northeastern, is more homogeneous than the Putnam Hill Limestone.
4. High heterogeneity exists between the Vanport Limestones in the three areas.
5. Equal, or perhaps greater, heterogeneity exists between Vanport Limestones and Shales within each of the three areas than between limestones or shales in different regions.
6. A χ^2 test showed that the northern Vanport resembles the Putnam Hill more than it does the southern Vanport. This conclusion is based on the 21 categories used for the tests rather than the biostratigraphic evidence which is not directly reflected in these data. The two conclusions, one environmental and provincial and the

other biostratigraphic, are not in conflict.

7. The Columbiana is less homogeneous than any other single-basin member, but more homogeneous than is the Vanport between its various basins. A large part of the Columbiana's apparent heterogeneity can probably be blamed on unusually large individual sample sizes.

8. The Washingtonville is more homogeneous than the Columbiana, but far less so than the Putnam Hill.

9. A large part of the real heterogeneity in both the Washingtonville and Columbiana Members probably comes from preservational differences.

Examples of some of these tests:

$$F = \frac{\text{Putnam Hill Ls. } \frac{343.6}{60} = 5.72}{\text{Southern Vanport Ls. } \frac{82.8}{42} = 1.97} = 2.90$$

$$\text{tab } F_{.10} = 1.47$$

Significantly greater homogeneity in the southern Vanport Limestone than in the Putnam Hill Limestone.

$$F = \frac{\text{Putnam Hill} = 5.72}{\text{Northeastern} = 3.0(-) \text{ Vanport Ls. } \left| \frac{59.7}{20} \right|} = 1.91$$

$$\text{tab } F_{.10} = 1.54$$

The northeastern Vanport Limestone also is significantly more homogeneous than the Putnam Hill Limestone.

A similar test involving the northwestern Vanport Limestone and the Putnam Hill Limestone showed that the former was also more homogeneous than the Putnam Hill, although in this case not significantly so. From these data it is apparent that each of the Vanport basins has a higher degree of internal consistency than the Putnam Hill, the most homogeneous unit overall.

Evaluation of testing.—The χ^2 and to a lesser degree the F tests seem ill-suited for treating these data. Inspection clearly indicated the faunal differences, and although the statistics in all cases supported these observations, too many falsely significant conclusions of differences resulted. Unquestionably, much of this operational inaccuracy could have been avoided by more carefully designed testing at the beginning of the study, but the necessary foundation of knowledge for the construction of this testing design did not exist *a priori*. Nevertheless, the χ^2 test, as used in this study seems overly sensitive for evaluating biologic data.

Late in the testing period the procedure of casting out the cells contributing most of the χ^2 value was instigated. By this method it was possible to remove everything contributing the differences in the first tests. Removing such heavy contributors as *Idio-gnathodus* vs. Others permitted more meaningful groups, which do show important differences, to not only remain in the test (previously they were too few to give expected values of 1.0 or greater when in the presence of the large categories), but also to assume their proper importance in the non-platform part of the fauna. No program to conveniently make such revisions is presently available, and the use with the present program is tedious, repetitious, and time

consuming. This manner of testing does hold considerable promise to treat data such as mine, and to derive more meaningful results.

V I T A

Glen Kenton Merrill was born in Columbus, Ohio, on 28 August, 1935, the son of the late Lee D. and Gladys Jaquith Merrill. He attended Bellpoint and Scioto Valley High Schools, Delaware County, Ohio and was graduated from the latter in 1953. He graduated from Ohio University, Athens, Ohio with a Bachelor of Science degree in geology in 1957. During the following two years he served on active duty as a first lieutenant in the United States Army. After leaving the military service he was employed by the U.S. Army Corps of Engineers in Huntington, West Virginia until entering The University of Texas in 1961. In 1964 he received the Master of Arts degree in geology from that institution. Following a temporary teaching position at Northwestern State College of Louisiana, Natchitoches, he entered Louisiana State University in the Fall of 1964.

While at Louisiana State University he has held the Humble Oil and Refining Company Fellowship (1965-1966). He is a member of $\Sigma\Xi$, the Paleontological Society, and the National Speleological Society.

In 1964 he married Stina Margareta Hellberg of Gamlakarleby, Finland. They have no children.

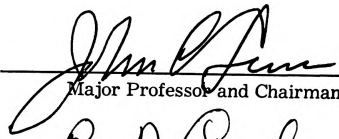
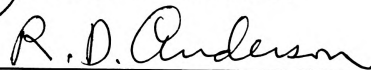
EXAMINATION AND THESIS REPORT

Candidate: GLEN K. MERRILL

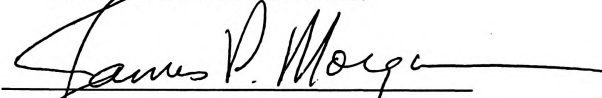
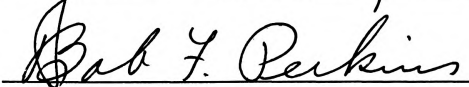
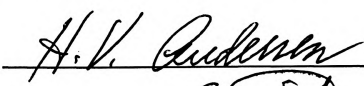

Major Field: GEOLOGY

Title of Thesis: ALLEGHENY (PENNSYLVANIAN) CONODONTS.

Approved:


Major Professor and Chairman

Dean of the Graduate School

EXAMINING COMMITTEE:

Date of Examination:

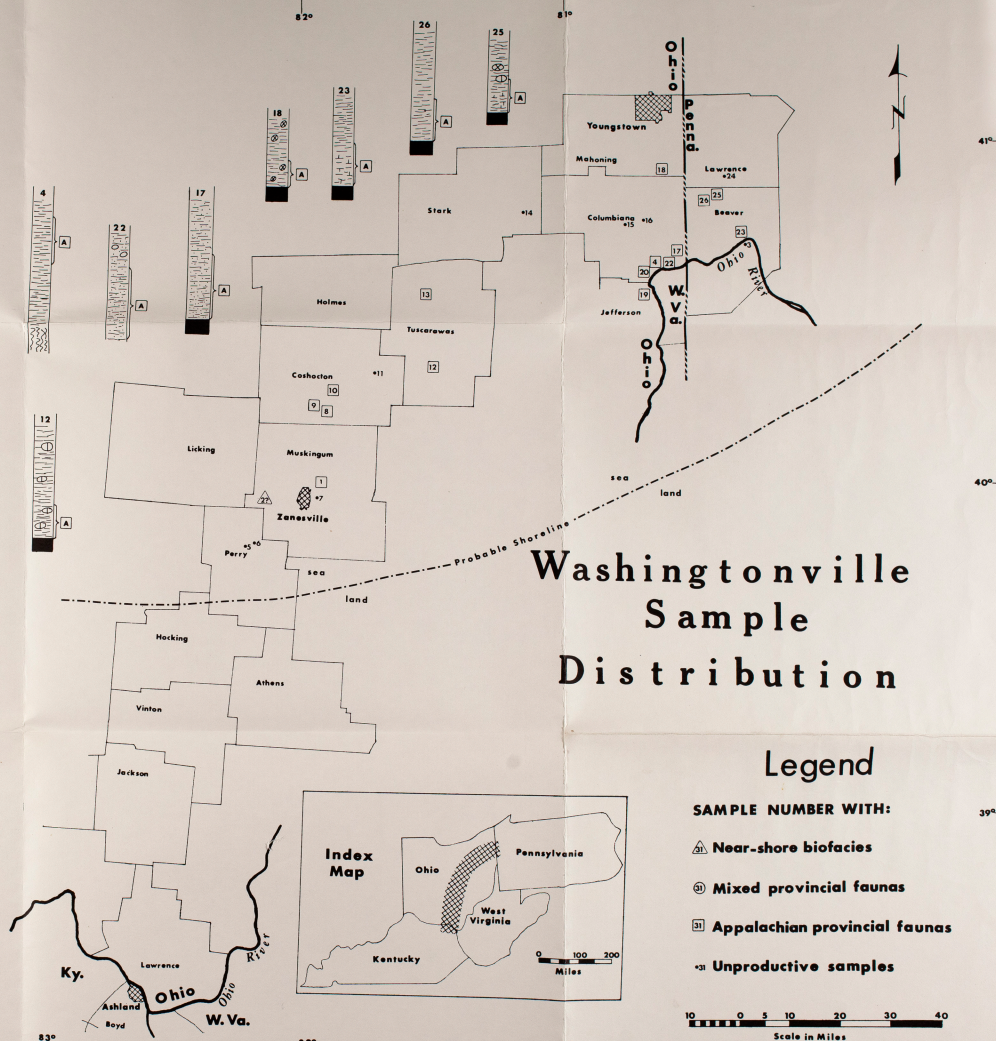
May 24, 1968

Stratigraphic Sections

- 31
A
B
C
- Numbered samples with lettered subsamples
and faunal symbols as on map
- 3
Conventional lithic symbols
- No horizontal scale

5
4
3
2
1
0

Vertical Scale (Feet)



Washingtonville Sample Distribution

Legend

SAMPLE NUMBER WITH:

- △ Near-shore biofacies
- ⑩ Mixed provincial faunas
- Appalachian provincial faunas
- * Unproductive samples

10 0 5 10 20 30 40
Scale in Miles

31

A

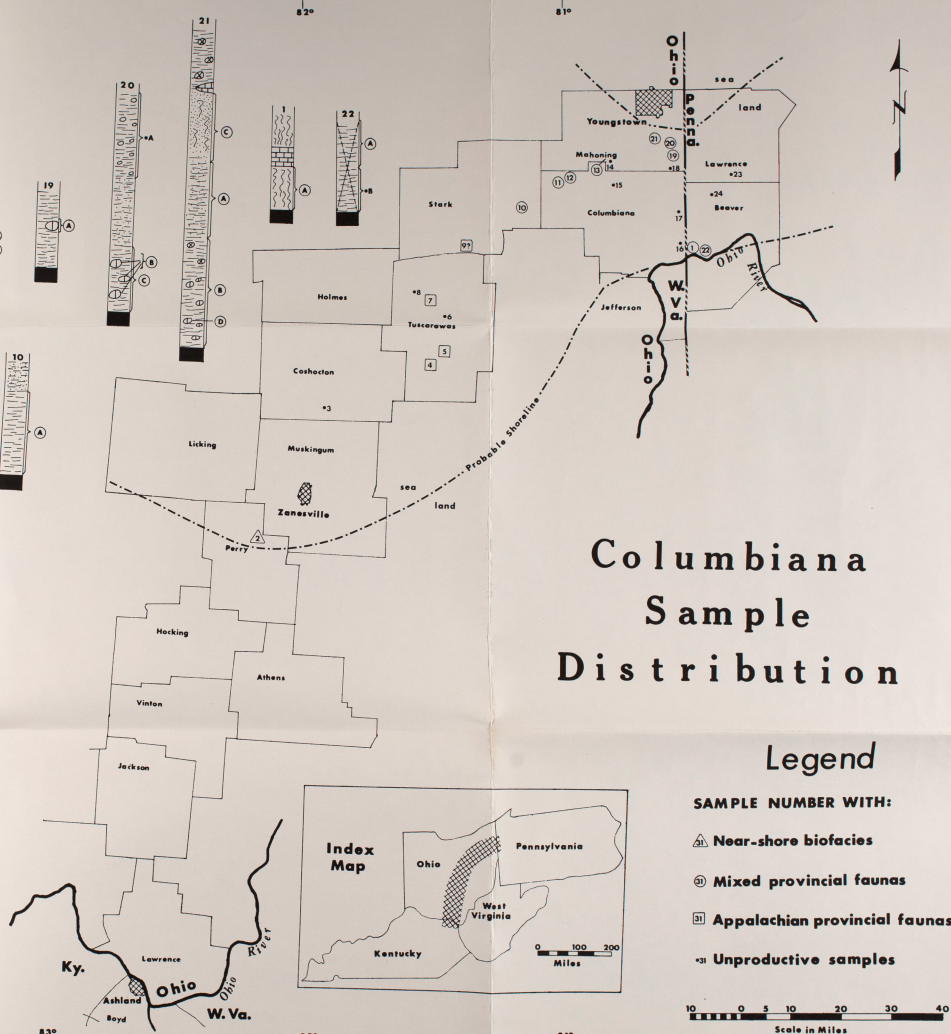
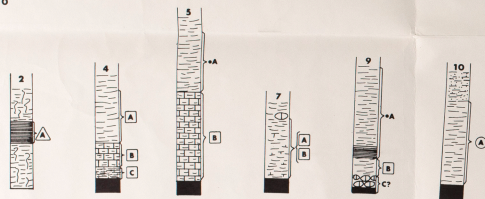
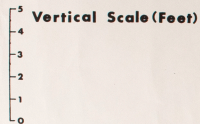
B

C

Numbered samples with lettered subsamples
and faunal symbols as on map

Conventional lithic symbols

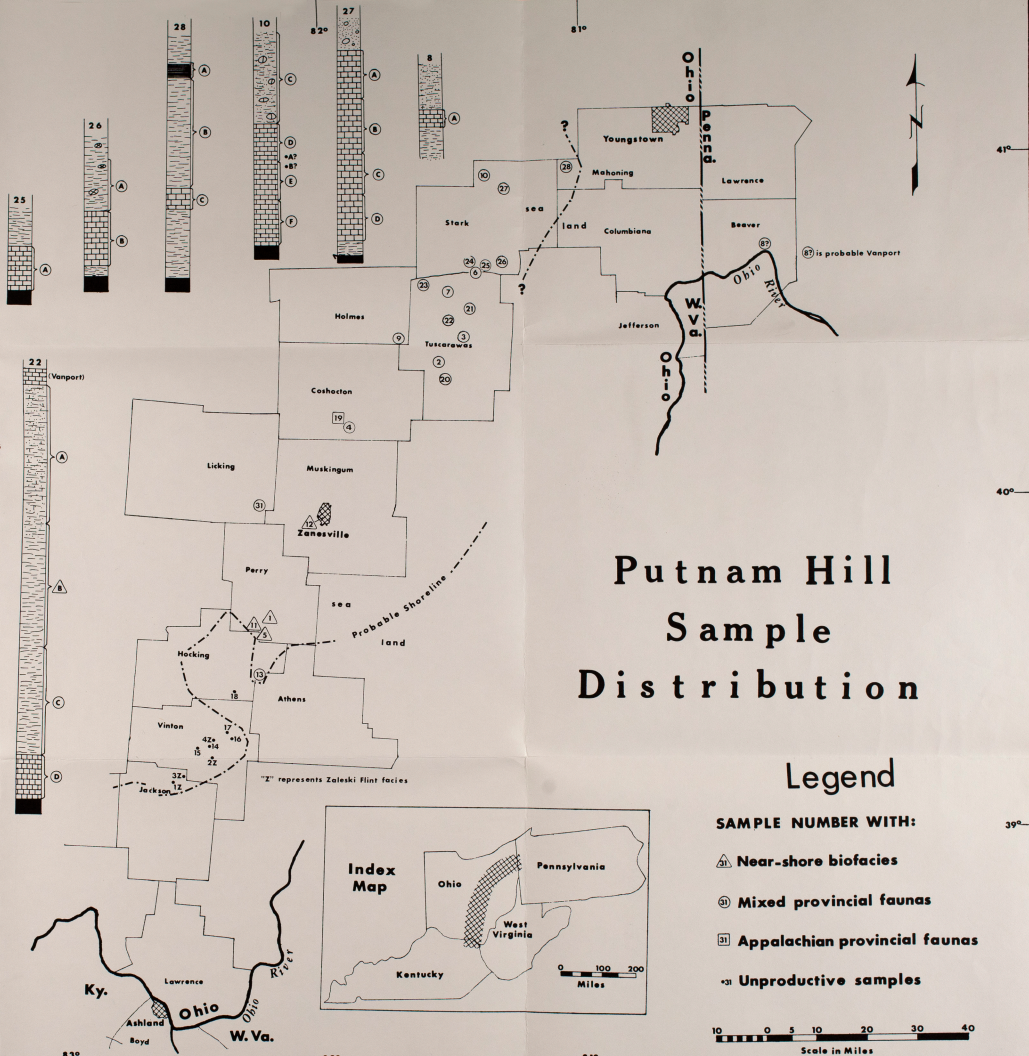
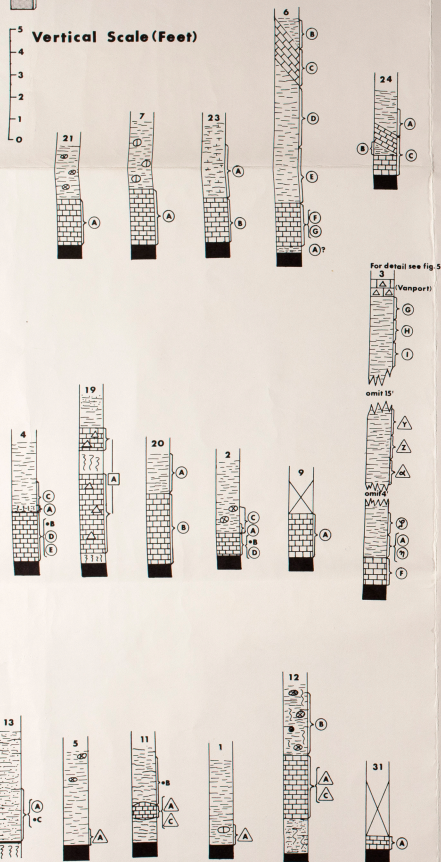
No horizontal scale



Stratigraphic Sections

- Numbered samples with lettered subsamples
and faunal symbols as on map
- Conventional lithic symbols
- No horizontal scale

Vertical Scale (Feet)



Putnam Hill Sample Distribution

Legend

SAMPLE NUMBER WITH:

- ▲ Near-shore biofacies
- ⑤ Mixed provincial faunas
- ③ Appalachian provincial faunas
- ✱ Unproductive samples

Scale in Miles

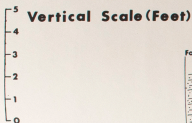
Stratigraphic Sections



Numbered samples with lettered subsamples and faunal symbols as on map

Conventional lithic symbols

No horizontal scale



For detail see fig. 5

3

+G

+A

+B

+C

+D

+E

+F

+H

+I

+J

+K

+L

+M

+N

+O

+P

+Q

+R

+S

+T

+U

+V

+W

+X

+Y

+Z

+AA

+AB

+AC

+AD

+AE

+AF

+AG

+AH

+AI

+AJ

+AK

+AL

+AM

+AN

+AO

+AP

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+JD

+JE

+JF

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+JH

+JI

+JJ

+JK

+JL

+JM

+JN

+JO

+JP

+JQ

+JR

+JS

+JT

+JU

+JV

+JW

+JX

+JY

+JZ

+KA

+KB

+KC

+KD

+KE

+KF

+KG

+KH

+KI

+KJ

+KK

+KL

+KM

+KN

+KO

+KP

+KQ